STERILITY IN WHEAT HYBRIDS. II. CHROMOSOME BEHAVIOR IN PARTIALLY STERILE HYBRIDS

KARL SAX

Maine Agricultural Experiment Station, Orono, Maine

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TABLE OF CONTENTS

INTRODUCTION 513
Previous cytological work with wheat 514
Material and methods 516
The chromosomes in the cultivated species of wheat 517
The chromosomes in sterile and partially sterile species hybrids 520
T. monococcum × *T. turgidum* 520
Emmer group × Vulgare group 521
The pollen grains in parents and F_1 hybrids 523
Discussion 526
Polyploidy in plant species 526
Genetic behavior of polyploid species 527
Chromosome behavior in certain partially sterile hybrids 530
Chromosome behavior and sterility 533
Sterility in wheat hybrids 535
The relation of chromosome behavior to sterility in wheat hybrids 535
The origin of tetraploidy and hexaploidy in wheat species 540
Chromosome number and adaptability in wheat species 541
The value of tetraploidy 543
Pollen-grain variability 545
SUMMARY 547
LITERATURE CITED 550

INTRODUCTION

The cultivated species of wheat can be divided into three definite groups according to their sterility relationships in interspecific crosses (SAX 1921). The Einkorn group contains only one species, *Triticum monococcum;* the Emmer group consists of *T. dicoccum*, *T. durum*, *T. turgidum*, and *T. polonicum;* the Vulgare group consists of *T. Spelta*, *T. vulgare*, and *T. compactum*. Einkorn crossed with members of the Emmer group or with members of the Vulgare group results in F_1 hybrids which are almost if not quite sterile. Species of the Emmer group crossed with species of the Vulgare group result in partially sterile F_1 hybrids. The species

within each group are inter-fertile. These sterility relationships are in accord with the recent taxonomic classifications (TSCHERMAK 1914, PERCIVAL 1921), with serological relationships as determined by ZADE (1914), and with VAVILOV's (1914) classification in respect to rust resistance.

In 1917 a study of the chromosomes of the wheat species and their hybrids was undertaken to determine the chromosome relationships in the cultivated species and the chromosome behavior in partially sterile hybrids. A knowledge of the chromosome behavior should be of value both in an analysis of the origin and relationships of the various species and in a genetic analysis of partially sterile hybrids. A cytological and genetic analysis of wide species crosses involving a certain amount of incompatibility, is especially important in view of EAST's (1921) conclusions in regard to the origin of important domesticated plants and animals.

PREVIOUS CYTOLOGICAL WORK WITH WHEAT

A comparatively large number of investigators have made cytological studies of the chromosome number in wheat. OVERTON (1893), KÖRNICKE (1896), DUDLEY (1908), NAKAO (1911), BALLY (1912, 1919) and PERCIVAL (1921) all report 8 as the haploid chromosome number in *T. vulgare*. SPILLMAN (1912) reports about 6 chromosomes in rye and about 40 in wheat. In all of these cases the papers are very poorly illustrated or are not illustrated at all. PERCIVAL and SPILLMAN present no drawings or figures to support their conclusions. In the other papers the drawings are not convincing, and if they faithfully represent the preparations the material was undoubtedly poorly fixed. The chromosomes are pictured as more or less shapeless masses and lack detailed shape and structure. Such an appearance is often due to poor fixation.

In 1917 the writer (SAX 1918) found about 28 chromosomes in the first division of the fertilized egg cell in *T. durum*. At about the same time SAKAMURA (1918) reported the following chromosome counts in wheat: *T. monococcum*, 14 (diploid); *T. durum*, *T. polonicum*, *T. turgidum* and *T. dicoccum*, 28; and *T. Spelta*, *T. vulgare* and *T. compactum*, 42. SAKAMURA's counts were made almost exclusively from preparations of root tips. The paper contains no illustrations of any kind.

The behavior of the chromosomes in partially sterile wheat hybrids has been described by KIHARA (1919). The hybrids used were *T. durum* × *T. vulgare*, *T. turgidum* × *T. compactum*, and *T. polonicum* × *T. Spelta*. The chromosome numbers of the parents were not determined, but were based on the work of SAKAMURA (1918). The F_1 hybrids were found to

have 35 diploid chromosomes, the sum of the gametic number of the parents. The behavior of the F_1 chromosomes in the reduction divisions is described as follows. At the time of the heterotypic division 14 bivalent and 7 univalent chromosomes are formed. The double chromosomes become oriented on the equatorial plate, but some of the single chromosomes may lie outside of the equatorial plate. As the double chromosomes divide normally and pass back to the poles, the single chromosomes become oriented on the plate, divide equationally and join the 14 chromosomes already at either pole. In the homotypic division 14 chromosomes pass to the poles leaving about 7 (often 5 or 6) chromosomes on the plate. These 7 chromosomes do not divide equationally at this time but pass apparently at random to either pole without dividing. Tetrads are usually formed normally but in some cases chromatic bodies are found in the cytoplasm of the one-nucleate microspores. Most of KIHARA's preparations were obtained from anthers, but somatic tissue was also used for determining the chromosome number in the F_1 plants.

KIHARA (1921) has also investigated the chromosome number in the F_2, F_3 and F_4 of the above partially sterile hybrids. In 8 F_2 plants the somatic chromosome number was found to vary from 31 to 42. In 16 F_3 plants the chromosome number varied from 28 to 41, and in 2 F_4 plants the chromosome number was 39 and 42. The number of univalent chromosomes was found to vary from 0 to 5. Some correlation was found in the F_3 between chromosome number and fertility,—the plants with a chromosome number approaching 42 were more fertile than plants with 38 or 39 chromosomes. The paper is illustrated with one plate of microphotographs which, although hardly adequate to support the author's conclusions, do indicate that he had excellent preparations.

It is evident that there is considerable dissension in regard to the chromosome number in wheat. Six investigators report 8 as the haploid chromosome number, one investigator reports about 40, two investigators report 14 for *T. durum*, and one investigator finds 7, 14 and 21 according to the species used. The last investigator (SAKAMURA) does not present any illustrations to support his counts. Since the value of a cytological paper is largely dependent on the character of the illustrations used, it is not surprising that SAKAMURA's results have been questioned (PERCIVAL 1921). In view of the different chromosome numbers reported by various investigators and the paucity of illustrations presented, a thorough cytological investigation of the chromosomes of wheat, with adequate illustrations, is justified.

MATERIAL AND METHODS

The following species of wheat were used in the present investigation:

Species	Variety
Triticum monococcum L.	*Hornemanni* Körn.
Cultural species	
T. durum Desf.	*hordeiforme* Körn. (Kubanka)
(*T. aestivum* L. subsp. *durum* (Desf.) Thell.)	
T. polonicum L.	*villosum* Körn. (Polish)
T. turgidum L.	*pseudo-cervinum* Körn. (Alaska)
(*T. aestivum* L. subsp. *vulgare* (Vill.) Thell. var. *turgidum* (L.) Druce)	
T. vulgare Vill.	*lutescens* Körn. (Marquis)
(*T. sativum* Lam. *T. aestivum* L. subsp. *vulgare* (Vill.) Thell.)	*erythrospermum* Körn. (Preston) *albidum* Körn. (Amby) (Bluestem)
T. compactum Host.	*Humboldtii* Körn. (Wash, Hybrid 143.)
(T. *aestivum* L. subsp. *vulgare* (Vill.) Thell. var. *compactum* (Host.) Sacc.)	
T. *Spelta* L.	
(*T. aestivum* L. subsp. *vulgare* (Vill.) Thell. var. *Spelta* (L.) Sacc.)	*album* Körn.

The chromosome behavior in the following F_1 hybrids was investigated.

(1) *T. monococcum* ♀ × *T. turgidum* ♂
(2) *T. compactum* ♀ × *T. durum* ♂
(3) *T. vulgare* (Amby) ♀ × *T. durum* ♂
(4) *T. durum* ♀ × *T. vulgare* (Amby) ♂
(5) *T. durum* ♀ × *T. vulgare* (Bluestem) ♂
(6) *T. vulgare* (Bluestem) ♀ × *T. durum* ♂
(7) *T. vulgare* (Bluestem) ♀ × *T. turgidum* ♂

For convenience the species of wheat may be divided into the three sterility groups, the Einkorn group, the Emmer (E) group, and the Vulgare (V) group. In measuring pollen grains several additional varieties of *T. vulgare* were used as well as *T. aegilops* Beauv.

The cytological work was started at Bussey Institution in 1917 but was interrupted until 1919 when it was resumed in Illinois. Since 1920 the work has been carried on at the Maine Agricultural Experiment Station and at the Bussey Institution.

Considerable difficulty was experienced at first in obtaining well fixed material. Often the chromosomes were found clumped together in such a way that accurate counts could not be made. SAKAMURA was unable to obtain well fixed anthers and used root tips for his preparations. Apparently none of the earlier investigators were able to get good fixation of wheat chromosomes at the time of the reduction divisions, if we may judge from the appearance of the illustrations. Poor fixation results in a grouping of the chromosomes into a varying number of shapeless masses of chromatin. I have frequently found approximately 8 such masses in poorly fixed material. In well fixed pollen mother cells the chromosomes are clearly defined, there is little shrinkage, and the cytoplasm shows great detail of structure.

The usual fixatives,—chrom-acetic acid, and Flemming's solution, gave good results in some cases, but the best results were obtained with a modified Bouin's solution developed by ALLEN (1916). This fixative has been used successfully in MCCLUNG'S laboratory when chromosome counts were desired. The modified Bouin's solution apparently prevents the clumping of the chromosomes and thus facilitates a detailed examination of the individual chromosomes.

In some cases the entire wheat head was fixed when it was about an inch long, but much better results were obtained when the anthers were dissected out. The best fixation was found where the fixative had to penetrate only a thin layer of tissue.

Sections were cut 10–12μ thick and were stained with Haidenhain's iron-haematoxylin. The drawings were done in ink and in all cases were made from single sections. I am greatly indebted to my wife for much assistance with the drawings, to Professor I. W. BAILEY for doing most of the work in preparing the photographs, and to Doctor EAST for valuable suggestions.

THE CHROMOSOMES IN THE CULTIVATED SPECIES OF WHEAT

The chromosomes in the cultivated species of wheat will be considered in order of their sterility and taxonomic relationships.

In Einkorn, *T. monococcum*, there are clearly 7 pairs of chromosomes in the pollen mother cells. At the time of diakinesis the paired chromosomes can be seen twisted about one another (figure 1). Often delicate fibers can be seen between the two members of a bivalent chromosome and between pairs of chromosomes. The bivalent chromosomes shorten, the nuclear membrane disappears, and the chromosomes become oriented on the equatorial plate. A polar view of the chromosomes at this stage is

shown in figure 2. In the heterotypic division the spindle fibers have a subterminal attachment to the chromosomes. The division proceeds regularly and there are no lagging chromosomes (figures 3, 4 and 38, plates 1 and 3). Occasionally a bivalent chromosome is drawn out into a long thread during division, as if the two members of the pair were firmly united at one end and were separated only by considerable tension. As the chromosomes pass back to the poles they become distinctly two-parted (figures 4 and 5). At this stage, the late anaphase, the chromosomes can be most readily counted. The numbers of chromosomes are clearly shown in the polar views of the late anaphase by figures 5 and 37. In the telophase the chromosomes lose their identity as individuals and then pass into the resting stage.

The chromosomes of the second or homoeotypic division are long, much like somatic chromosomes, and are difficult to count. The second division is normal and there are no lagging chromosomes (figure 6). This division takes place at right angles to the heterotypic division and in the same plane so that the resulting microspores of each tetrad are in one plane.

In the species of the Emmer group,—*T. durum*, *T. turgidum*, *T. polonicum* and *T. dicoccum*,—there are 14 gametic chromosomes. In *T. durum* and *T. polonicum* the number has been determined in the pollen mother cells, but in other species of this group the number was determined only approximately from somatic counts.

The 14 pairs of chromosomes in the diakinesis of *T. durum* are shown in figure 7. In most cases the double nature of the bivalents is clearly evident. Often some pairs appear to be longer than others but such differences may be due partly to different stages of contraction. The chromosomes on the equatorial plate are shown in figures 8 (*T. polonicum*) and 9 (*T. durum*) and the anaphase is shown in figure 39. When well fixed the chromosomes can be easily counted at these stages. A side view of the metaphase of the heterotypic division is shown in figure 10. The division is regular and there are no lagging chromosomes at any time (figure 11). The two-parted chromosomes on reaching the poles pass into the resting condition and a cell plate is formed (figure 12). The second division is normal and the four cells of the tetrad are formed in one plane (figure 13).

There are 21 haploid chromosomes in the species of the Vulgare group. The chromosomes in the diakinesis are often grouped around the nucleolus, and owing to the relatively large number it is not easy to count them at this stage. Accurate counts can be obtained from the metaphase of the heterotypic division. A polar view of the metaphase of *T. Spelta* is shown

in figure 14 and a similar view of the chromosomes of *T. vulgare* is shown in figures 15 and 40. The subterminal attachment of the spindle fibers together with the anastomosis of certain parts of the bivalent chromosomes results in unusual distortion of the chromosomes at the time of division (figure 16). The free ends of the chromosomes are usually short and thick, while the portions between the fiber attachment and the united ends are often drawn out into thin threads. There are no lagging chromosomes at any time either in the anaphase or telophase (figures 17, 19 and 44). The chromosomes in the late anaphase can be easily counted (figure 18). The chromosomes in the second division are very long and can be counted only with difficulty. The approximate number may be counted in figure 20, which is the metaphase of the second division in *T. vulgare*. The division is normal and the tetrads are formed as in the other groups of species.

There is apparently little difference in the size of the individual chromosomes within or between species. Often several long bivalents can be seen in diakinesis in the Emmer and Vulgare groups, but the number of these varies even in the same individual plant. In the side views of the metaphase certain chromosomes are longer than others, but here again the number of very long chromosomes varies and it is probable that the longer chromosomes have no greater volume than some of the shorter ones. In the figures it appears that the individual chromosomes of Einkorn are larger than the chromosomes of the other species, but such an appearance may be entirely due to differences in fixation and staining. The preparations of Einkorn were stained much more deeply than preparations of the other species.

In general there is some correlation between chromosome number and cell size, as indicated by the size of the pollen mother cells in the different species. Often, however, the cells are cut in such a way that a cross section does not indicate their relative volume. Differences in stages of development as well as differences in fixation may also cause differences in apparent size of cells even in the same species.

The chromosomes of rye have never been pictured, so several figures of rye are presented in figures 41A and 41B. The twisted pairs of chromosomes in diakinesis is especially well shown in figure 41A. In several cases all 7 chromosomes can be counted even at the stage of diakinesis.

THE CHROMOSOMES IN STERILE AND PARTIALLY STERILE SPECIES HYBRIDS

T. monococcum × *T. turgidum*

In the cross of Einkorn × Alaska the F_1 plant has 21 somatic chromosomes, 7 contributed by the Einkorn parent and 14 contributed by the Alaska parent. At the time of the first reduction division about seven pairs of chromosomes are formed, leaving approximately 7 single chromosomes. Presumably the 7 Einkorn chromosomes pair with 7 of the Alaska chromosomes, leaving 7 single or univalent chromosomes contributed by the Alaska parent. The bivalent chromosomes orient themselves on the equatorial plate, but the single chromosomes are usually found at or near the poles of the spindle figure,—seldom on the equatorial plate. In figure 22 there are 6 pairs of chromosomes shown on the heterotypic plate and one pair which has divided. Four single chromosomes lie at one pole and three at the other, a total of 7 single chromosomes. The number of single chromosomes at the poles varies somewhat, but the total number is approximately 7 in most cases (table 1).

TABLE 1

Assortment of single chromosomes in the heterotypic division of the F_1 Einkorn × Alaska.

Number of single chromosomes at either pole	4 3	4 4	5 3	4 2	5 2	6 1	5 4	3 2	6 3	5 6
Total singles	7	8	8	6	7	7	9	5	9	11
Actual frequency	8	4	4	3	3	3	2	1	1	1
Theoretical frequency	17				10	3				

The number of single chromosomes may vary due to segmentation, or they may lie on the plate with the double chromosomes in some cases. It is also possible that less than 7 bivalent chromosomes are formed, in which case the total number of singles would be 9 or 11. In general, however, the chromosome number is approximately 7 and the distribution of about equal numbers of single chromosomes to either pole occurs with greatest frequency as expected.

The single chromosomes remain at the poles while the bivalent chromosomes divide and join the single chromosomes. The total number of chromosomes at either pole is then usually about 10 or 11 (fig. 23). As the members of the bivalent chromosomes pass to the pole they split

longitudinally as usual (figure 24). All chromosomes both single and double are grouped together in the telophase (figure 25).

In the homoeotypic division approximately ten chromosomes are found at the metaphase (figure 27). These chromosomes are long and curved. They consist of the 7 divided bivalents plus 0 to 7, but usually 2 to 5, univalent chromosomes. Since the univalents did not divide during the heterotypic division they would be expected to divide normally in the homoeotypic division. The actual behavior of the chromosomes during the second division is difficult to determine owing to the length of the chromosomes and the paucity of critical stages. The division appears to be normal, however, and seldom were any lagging chromosomes found (figure 26). The tetrads are formed as in the case of the parental species and in comparatively few cases are chromatin granules found outside of the nuclei. The tetrads separate into one-nucleate pollen grains which appear to be normal. Very few of the one-nucleate pollen grains develop normally, however, and only about 2 to 3 percent of the mature pollen grains appear normal. Probably none of them is functional.

In a few cases the univalents were found on the heterotypic plate after the bivalents had divided, indicating that the behavior of the univalents in the reduction division may vary in different individuals.

Emmer group × Vulgare group

In crosses between members of the Emmer group and members of the Vulgare group the sum of the gametic numbers of chromosomes is 35. Such F_1 plants will have 14 chromosomes contributed by one parent and 21 chromosomes contributed by the other parent. In the pairing of the chromosomes for reduction the 14 chromosomes of the Emmer group presumably pair with 14 chromosomes of the Vulgare group, leaving 7 univalent Vulgare chromosomes. At any rate in diakinesis there are about 14 bivalents and 7 univalents. The bivalent and univalent chromosomes can easily be distinguished in the metaphase of the heterotypic division. A polar view of the metaphase of the F_1 of Amby (V) × Kubanka (E) is shown in figures 28 and 42. The 7 univalent chromosomes are long, slender and V-shaped, while the bivalent chromosomes are like the bivalents in the normal heterotypic division in the parent species. A similar stage is shown in the F_1 of Bluestem (V) × Alaska (E) in figure 29. The univalents are usually arranged on one side of or around the group of bivalents.

Some of the single chromosomes often lie outside of the equatorial plate and appear to be distributed more or less at random in the division figure (figure 30). Usually only two or three single chromosomes can be seen outside of the equatorial plate in a side view, but in a polar view all of the univalents may lie outside of the group of bivalents. As the bivalents divide and pass to the poles the univalent chromosomes become oriented on the equatorial plate (figures 31-34, 43 and 45). The univalents may vary in number due possibly to the failure of all 14 chromosomes to pair, or to the premature or accidental passage of single chromosomes to the poles (figure 30).

TABLE 2

Number of lagging single chromosomes in the heterotypic division of F_1 of Emmer group × Vulgare group.

Number of lagging chromosomes	4	5	6	7	8	9
Frequency	1	3	7	22	2	1

Table 2 was prepared from well fixed division figures before all of the univalents had separated and where the figure was apparently intact. In the majority of cases 7 lagging univalents were found (figures 32 and 34). In one case 9 single chromosomes appeared to be present (figure 31), but at least one univalent may be segmented into two parts. The univalents are frequently somewhat constricted in the centers where the spindle fibers are attached. The grouping of the bivalents on one side of the spindle is often found (figure 33). The 14 chromosomes at the poles, resulting from division of the bivalents, can frequently be counted with little difficulty, but it is difficult to picture them because they are so compactly grouped.

The segmented univalent chromosomes divide and pass to the poles (figure 35). In most, if not in all cases, there are no chromosomes left free in the cytoplasm, but all are grouped together in the telophase (figures 36 and 46). The daughter nuclei thus formed pass into the resting stage.

In the second division some univalent chromosomes are found outside of the equatorial plate in the metaphase (figure 47). In the late anaphase or telophase univalent chromosomes are found lagging after most of the chromosomes have reached the poles (figures 37 and 48). The number of lagging chromosomes varies, with the mode at 5. Perhaps some of the chromosomes at the poles in the metaphase (figure 47) remain there

and fail to take their place on the plate, or single chromosomes may accidentally pass to the poles with the original members of the bivalents. The following table shows the distribution of the single lagging chromosomes in the second division.

TABLE 3

Number of lagging chromosomes in the homoeotypic division. Vulgare group × Emmer group.

Number of lagging chromosomes	2	3	4	5	6	7
Frequency	1	3	5	10	5	2

The lagging chromosomes do not divide equationally but pass apparently at random to either pole. Thus the four microspores each contain 14 chromosomes presumably contributed by both parents according to chance and from 0 to 7 additional chromosomes of the Vulgare parent, the latter number also depending on chance distribution. The fact that the univalent chromosomes divide but once, equationally of course, while the bivalents divide twice in the course of gametogenesis, is in accord with the usual conception of the nature of the reduction divisions.

In some cases the lagging chromosomes fail to go back to the poles and several chromosomes may lie outside of the reconstructed nucleus, usually in the vicinity of the newly formed cell wall. As a rule, however, microspores are formed which have no chromatic material in the cytoplasm outside of the nucleus. These one-nucleate pollen grains appear to be entirely normal so far as the morphological structure is concerned. In many cases, however, they are unable to develop into normal pollen grains. About 20 percent of the pollen of the F_1 plants resulting from Emmer group × Vulgare group crosses is obviously imperfect as indicated by smaller size and meager contents. Undoubtedly a larger percentage is not functional because of physiological or other imperfections in pollen grains that appear morphologically perfect.

THE POLLEN GRAINS IN PARENTS AND F_1 HYBRIDS

There is a striking correlation between chromosome number and the size of the pollen grains in the wheat species studied. Such a relation would be expected if BOVERI'S conclusions concerning chromosome number and cell size have a general application. The pollen grains are especially good for testing such relationships because they consist of only several cells, their volumes are easily determined, and they can be meas-

TABLE 4

Size and variability of pollen grains of wheat varieties and species and of some F_1 hybrids. 1921 data.

VARIETY OR F_1 HYBRID		DIAMETER IN MICRONS (CLASS CENTERS) 37.5	39.0	40.5	42.0	43.5	45.0	46.5	48.0	49.5	51.0	52.5	54.0	55.0	57.0	58.5	60.0	61.5	63.0	64.5	66.0	67.5	N	MEAN	σ	C. V.	VOLUME CU. μ
Aegilops ovata	W	1	8	15	15	16	5	2	1														63	43.55±.18	2.12±.13	4.87±.29	53,000
	L							1	3	5	19	20	9	5	1								63	53.55±.15	1.80±.11	3.35±.20	
Einkorn		3	12	23	33	44	13	6	4														138	44.02±.13	2.19±.09	4.98±.20	45,000
Kubanka	E						1	3	13	19	20	22	10	4	3	1							96	51.22±.18	2.62±.13	5.12±.24	70,000
Alaska	E						2	4	8	13	14	23	22	7	1	1							95	51.76±.19	2.68±.13	5.18±.25	73,000
Polish	E					1	5	6	19	17	27	31	5	1	1								113	50.34±.16	2.47±.11	4.90±.22	67,000
Emmer	E						2	2	8	19	29	26	11	9	4	2							112	51.70±.17	2.62±.12	5.07±.23	72,000
Spelt	V								2	2	4	13	15	17	11	12	8	3		1			88	55.59±.23	3.15±.16	5.67±.28	90,000
Marquis	V									2	5	18	20	27	18	5	4						99	54.91±.15	2.27±.11	4.14±.20	87,000
Amby	V									1	5	14	16	26	15	8	4	2					91	55.30±.17	2.47±.12	4.46±.22	89,000
Preston	V									2	4	21	23	25	20	5	5						105	54.92±.15	2.29±.11	4.17±.19	87,000
Royalton White	V									1	5	15	24	33	14	7	2						101	54.92±.14	2.06±.10	3.75±.14	87,000
Kota V × Royalton	V							1	1	3	7	12	17	21	18	8	4		1				93	54.95±.20	2.85±.14	5.19±.25	87,000
Spelt V × Marquis	V			1	1	1	2	1	6	4	8	9	12	18	17	13	16	5	4	1			119	55.37±.29	4.67±.20	8.44±.37	89,000
Polish E × Emmer	E				1	3	2	7	8	10	13	18	15	12	9	1	1		1				101	51.94±.26	3.85±.19	7.40±.35	73,000
Emmer E × Polish	E		1	1	2	2	4	9	9	9	24	12	10	10	5	3	2	2					105	52.73±.29	4.37±.20	8.28±.39	77,000
Kubanka E×Marquis	V	1	2	3	4	8	8	4	4	3	7	15	10	6	7	11	12	6	4	4	1		120	53.04±.43	6.39±.30	13.07±.58	78,000

ured at the same stage of development. The size and variability of the pollen grains of most of the wheat species and of F_1 hybrids between varieties, compatible species, and members of different sterility groups are shown in table 4.

In *T. aegilops ovata* the pollen grains were not spherical and two dimensions were taken to determine the volume. In all other cases the pollen grains were approximately spherical, so only the diameter was measured. In all cases only the apparently good pollen grains were used. Only in the partially sterile hybrid Kubanka × Marquis, was the percentage of obviously poor pollen grains more than 1 to 2 percent. The pollen grains were mounted in lactic acid and were measured with an ocular micrometer.

In Einkorn with 7 chromosomes the mean volume of the pollen grains, measured in thousands of cubic microns, is 45. In the species of the Emmer group with 14 chromosomes the mean volume of the pollen grains is about 70. In the species of the Vulgare group the mean volume of the pollen grains is about 88. The F_1 hybrids resulting from crossing members of the Vulgare group, have pollen grains of about the same size as the parents, and a similar condition obtains for F_1 hybrids within the Emmer group.

Not only is there a consistent and significant relation between pollen-grain size and chromosome number in the various species groups, but there is also a consistent relation between heterozygosis and pollen-grain variability. In the homozygous parents the coefficient of variability for pollen-grain diameter ranges from $3.75 \pm .14$ to $5.67 \pm .28$. In the cross, Kota × Royalton White, both parents belong to the same species, *T. vulgare*, and the pollen-grain variability is little if any greater than for the parents. In the cross, Spelt × Marquis, the parents belong to different species, but to the same sterility group, and the pollen of the F_1 is significantly more variable than for the parents or the preceding varietal cross. The reciprocal crosses between Polish and Emmer also involve different species, but only one sterility group, and the pollen-grain variability in the F_1 is significantly greater than in the parents. The F_1 resulting from Kubanka × Marquis has pollen grains almost three times as variable as the parent species. In this case the parents belong to different sterility groups and the F_1 is partially sterile. The striking increase in pollen-grain variability is not due to obviously aborted pollen grains because only the apparently good pollen grains were measured It will be noted that the distribution is not especially skew or bimodal as

would be the case if the increased variability were due only to poorly developed or aborted pollen.

Apparently environmental conditions may cause differences in pollen-grain size. The size of the pollen grains in 1920, measured in thousands of cubic microns, was 72 for Einkorn, 94 for the Emmer group and 114 for the Vulgare group. The relative sizes of the pollen grains of the three sterility groups was about the same in 1920 and 1921.

Pollen-grain size and chromosome number are also correlated in a similar manner in the species of oats.

DISCUSSION

Polyploidy in plant species

The occurrence of the gametic chromosomes in multiples of 7 in the species of wheat suggests that the Emmer and the Vulgare groups are tetraploid and hexaploid forms, respectively, of an original type with 7 chromosomes. The origin of new species by tetraploidy in other genera would tend to support such a view. *Oenothera gigas*, a mutant from *Oe. Lamarckiana*, is the best known case of tetraploidy in plants. The chromosome number of the mutant was found to be 28 as compared with 14 for the parental species (LUTZ 1907). Miss DIGBY (1912) found a tetraploid form of *Primula kewensis* with 36 somatic chromosomes. Tetraploidy has been found recently in Datura (BLAKESLEE, BELLING AND FARNHAM 1920). In all of the above cases tetraploidy has occurred while the species were under observation. The hereditary behavior of the tetraploid plants shows a doubling of genetic factors and thus supports the cytological observations.

Chromosome duplication has also been found in other species which have not been under such close observation and which have not been tested by breeding experiments. In Hieracium there are species with 18, 27, 36 and 42 somatic chromosomes (ROSENBERG 1917). In Crepis species are found with 6, 8, 10, 16, 18, 24 and 42 somatic chromosomes. ROSENBERG (1920) believes that the species with the higher chromosome numbers are caused by the duplication of one or more pairs of the chromosomes in the primary species, *C. virens*, with 3 pairs of chromosomes. In the species with 8 chromosomes the medium-sized pair of chromosomes is reduplicated while in the "*gigas*-mutant," *C. Reuteriana*, each pair is reduplicated. In the genus Rosa species are found with 14, 21, 28, 35 and 42 somatic chromosomes (TÄCKHOLM 1920).

In Chrysanthemum TAHARA (1915) finds in different species haploid numbers of 9, 18, 27, 36 and 45. GATES (1913) lists a number of other cases of tetraploidy in plant and animal species and additional cases have been found in the past few years.

Genetic behavior of polyploid species

In tetraploid plants the doubling of the chromosome number results in a duplication of the genetic factors. Thus tetraploidy can be detected not only by chromosome counts but also by the genetic behavior of hybrids of tetraploid races. If the reduplicated chromosomes of a tetraploid or hexaploid species, or to use BLAKESLEE'S (1920) terminology, the members of the tetrasomic and hexasomic sets, assort in pairs, the usual 15 : 1 or 63 : 1 ratios will result in F_2. If, however, the chromosomes of a tetrasomic or hexasomic set assort at random in an F_1 hybrid a 35 : 1 or 399 : 1 ratio will be found in the F_2. Furthermore, in such tetraploid and hexaploid plants the number of recessive factors may often exceed the number of dominant factors in heterozygous individuals in F_2 hybrids. There is evidence that in some cases either allelomorph of a pair of characters may be dominant if an excess of factors of one character are present. In the case of starchy and corneous endosperm in maize, HAYES and EAST (1915) have found that the character borne by the mother plant was always dominant, due presumably to the dominance of the two factors contributed by the mother, as a result of polar fusion, over the single factor contributed by the male parent. In Drosophila it has been found that the two recessive genes for vermilion and sable dominate the normal allelomorphs. When the mutant and normal factors are in equal numbers the normal is dominant (MORGAN 1919). Sex in Drosophila is determined by the ratio of X chromosomes to autosomes. BRIDGES (1921) has found that the ratio of 2 X : 2 sets of autosomes produces a female while 1 X : 2 sets of autosomes produces a male and the ratio 2 X : 3 sets of autosomes produces an intermediate condition, the intersex. There is also evidence that characters other than sex are also influenced by chromosome ratios.

It is possible that an excess of recessive factors may be dominant over the normally dominant factors in many cases, but because such cases become evident in diploid species only in endosperm characters, or in case of non-disjunction or other unusual chromosome behavior, they are seldom detected. The dominance of the normally recessive character would never occur in diploid plants except in endosperm characters, but in triploid, tetraploid and hexaploid plants such a relationship of dominant

and recessive characters would be found. Although few such cases have been discovered it is a possibility to be considered. We have then two possible causes for unusual genetic ratios in polyploid plants,—random assortment of chromosomes and reversed dominance due to an excess of recessive factors. The gametic constitution and genetic ratios for various combinations of diploid, tetraploid, and hexaploid hybrids are given in table 5.

In case of random assortment of chromosomes in a tetrasomic set the F_2 ratio becomes 35 : 1 instead of 15 : 1 which is found if the chromosomes assorted in pairs. In the hexasomic set random assortment would result in an F_2 ratio of 399 : 1 and in most F_2 plant populations such a segregation would not be detected. It is also obvious that a tetraploid individual can never be homozygous for a single factor in case of random chromosome assortment and in hexaploid individuals neither one nor two factors can exist in the homozygous condition. If, then, a mutation occurs in a single chromosome of a hexasomic set in which the chromosomes assort at random the homozygous condition will be attained only when all 3 chromosomes of the set are either dominant or recessive. In a homozygous hexaploid race one- and two-factor differences will not be found with random assortment of the members of the hexasomic sets.

An examination of the hereditary behavior of tetraploid species indicates that in most cases studied the chromosomes assort at random in the tetrasomic sets. MULLER (1914) in analyzing GREGORY'S data on tetraploid Primulas concluded that where more than 2 factors are present, which are normally allelomorphic to each other, the pairing of these allelomorphs usually takes place at random. He interpreted the ratio of 4.5 : 1 in a back-cross as a 5 : 1 ratio expected, rather than a 3 : 1 ratio, and showed that the ratio of 119 : 4 in F_2 may be interpreted as a 35 : 1 ratio rather than a 15 : 1 ratio proposed by GREGORY. MULLER'S analysis of GREGORY'S data indicates that in the tetraploid Primula the chromosomes of a tetrasomic pair assort at random. In Datura the duplicated chromosomes of the Poinsettia mutant apparently assort at random according to BLAKESLEE, BELLING AND FARNHAM (1920). Unusual ratios are obtained because the Poinsettia character is not carried by the pollen to any significant extent. In *Oenothera gigas* certain races when selfed produce 1 to 2 percent *nanella* mutants and pedigrees are found approaching a 3 : 1 ratio. BLAKESLEE'S (1921) analysis of DE VRIES'S data indicates that the 1 to 2 percent *nanella* segregates are recessive in a 35 : 1 ratio, and the fact that dominants from a 3 : 1 ratio throw 3 : 1 ratios or 35 : 1 ratios supports BLAKESLEE'S

TABLE 5

Result of crossing diploid, tetraploid, and hexaploid species when (1) the allelomorphic chromosomes unite in homologous pairs, and when (2) they pair at random. The F_2 ratios, R : r, are given when (a) an Rrr genotype appears as an R phenotype and when (b) an Rrr genotype appears as an r phenotype.

		CHROMOSOMES UNITE IN HOMOLOGOUS PAIRS			CHROMOSOMES OF POLYSOMIC SET PAIR AT RANDOM		
Parents	F_1	F_1 gametes	(a)	(b)	F_1 gametes	(a)	(b)
$R_1R_2 \times r_1$ $R_1R_2 \quad r_1$	R_1R_2 r_1	R_1R_2-r_1-R_2-r_1R_2	15 : 1	13 : 3	R_1R_2-R_1r_1-r_1R_2-r_1-R_1-R_2	35 : 1	31 : 5
$R_1 \times r_1r_2$ $R_1 \quad r_1r_2$	R_1 r_1r_2	R_1-r_1r_2-R_1r_2-r_1	3 : 1	3 : 5	r_1r_2-r_1R_1-r_2R_1-R_1-r_1-r_2	3 : 1	13 : 23
$R_1R_2 \times r_1r_2$ $R_1R_2 \quad r_1r_2$	R_1R_2 r_1r_2	R_1R_2-R_1r_2-r_1R_2-r_1r_2	15 : 1	11 : 5	R_1R_2-R_1r_2-r_1R_2-r_1r_2-R_1r_1-r_1R_2	35 : 1	3 : 1
$R_1R_2R_3 \times r_1r_2r_3$ $R_1R_2R_3 \quad r_1r_2r_3$	$R_1R_2R_3$ $r_1r_2r_3$	$R_1R_2R_3$-$r_1R_2R_3$-$R_1r_2R_3$ $R_1R_2r_3$-$r_1r_2r_3$-$R_1r_2r_3$ $r_1R_2r_3$-$r_1r_2R_3$	63 : 1	42 : 22	$R_1R_2R_3$-$r_1R_2R_3$-$R_1r_2R_3$-$R_1R_2r_3$ $r_1r_2r_3$-$R_1r_2r_3$-$r_1R_2r_3$-$r_1r_2R_3$ $R_1R_2r_3$-$r_1R_2r_3$-$R_1R_2r_2$ $R_2R_1r_1$-$r_2R_2r_3$-$r_2R_1r_1$-$R_2R_2r_3$ $R_3R_1r_1$-$r_3R_2r_2$-$r_3R_1r_1$-$R_3R_2r_2$	399 : 1	282 : 118
$R_1R_2r_3 \times r_1r_2r_3$ $R_1R_2r_3 \quad r_1r_2r_3$	$R_1R_2r_3$ $r_1r_2r_3$		15 : 1	22: 42		24 : 1	2 : 3
$R_1r_2r_3 \times r_1r_2r_3$ $R_1r_2r_3 \quad r_1r_2r_3$	$R_1r_2r_3$ $r_1r_2r_3$		3 : 1	0 : 64		3 : 1	0 : 400
$R_1R_2R_3 \times R_1r_2r_3$ $R_1R_2R_3 \quad R_1r_2r_3$	$R_1R_2R_3$ $R_1r_2r_3$		64 : 0	15 : 1		400 : 0	24 : 1
$R_1R_2R_3 \times r_1r_2$ $R_1R_2R_3 \quad r_1r_2$	$R_1R_2R_3$ r_1r_2		63 : 1	3 : 1		399 : 1	324 : 76
$R_1R_2 \times r_1r_2r_3$ $R_1R_2 \quad r_1r_2r_3$	R_1R_2 $r_1r_2r_3$		15 : 1	26 : 38		3 : 1	1 : 24

conclusions. BLAKESLEE suggests that all of the Oenothera mutants are caused either by chromosomal duplication or are due to crossovers from balanced lethals as suggested by MULLER (1918). In connection with MULLER's hypothesis, however, it may be suggested that if we accept the telosynaptic method of reduction described in Oenothera by DAVIS (1911) and GATES (1915) and at the same time accept the mechanical chiasma-type hypothesis of crossing over, there would be little or no opportunity for crossing over to occur.

In the case of Oenothera, Primula and Datura, the tetraploid forms have originated in experimental cultures and in all cases the chromosomes of a tetrasomic set appear to assort at random. In wheat there is no evidence that random assortment of chromosomes takes place in tetrasomic and hexasomic sets. The results of NILSSON-EHLE (1909), the HOWARDS (1912) and GAINES (1917) all show ratios closely approximating 15 : 1 or 63 : 1 in wheat hybrids involving several independent similar, or possibly identical, factors for the same character. Segregates can be obtained from the F_2 of a trihybrid, which are homozygous for 1 or for 2 factors, an impossible result in case of random chromosome assortment. In the segregation of capsule form in Bursa as described by SHULL (1914) the F_2 ratio approximately 24 : 1 might suggest a random assortment of chromosomes in a hexasomic set with 4 dominant factors, but such a parental type would not exist in a homozygous condition and the behavior of the F_2 segregates proves that 2 factors are involved which assort in pairs. The fact that a character may be determined by several factors does not necessarily indicate that these factors are the result of chromosome duplication.

In both wheat and Bursa multiple factors, presumably allelomorphic and in duplicate chromosomes, do not assort at random as they do in case of tetraploid Oenotheras, Primulas and Daturas. The difference in chromosome behavior may be due to the recent origin of tetraploidy in some species as compared with wheat. It is also possible that the increased chromosome number is not due to duplication of the fundamental chromosome number, or if it is, the individual chromosomes may have changed so that they assort in pairs.

Chromosome behavior in certain partially sterile hybrids

Hybrids between diploid and tetraploid, and between tetraploid and hexaploid, wheat species are completely or partially sterile, and irregular chromosome behavior occurs in the reduction divisions. In the F_1 hybrids between Einkorn with 14 chromosomes and a member of the Emmer

group with 28 chromosomes there are 7 bivalents and 7 univalents in the heterotypic spindle. The bivalents divide normally in both meiotic divisions while the singles pass at random, without dividing, to either pole in the first division and presumably divide in the second division. In hybrids between members of the Emmer group with 14 chromosomes with members of the Vulgare group with 21 chromosomes the 14 pairs of chromosomes divide as usual in meiosis while the 7 univalents lag behind but ultimately divide equationally in the first division and pass at random, without dividing, to either pole in the homoeotypic division. A comparison of chromosome behavior and sterility in similar hybrids in other genera is of interest.

In Drosera (ROSENBERG 1909) the chromosomes of the F_1 of a cross between a species with 10 haploid chromosomes and a species with 20 chromosomes, behave like the chromosomes in the Einkorn × Alaska cross in wheat. In the reduction division 10 bivalents and 10 univalents are found. The single chromosomes lag and apparently go at random to either pole without dividing. The second reduction division is not described.

In the F_1 of *Oenothera lata* × *Oe. gigas* GATES (1909) found the chromosome number to be 20 or 21, the sum of the gametic numbers of the parents. In the reduction division 10 or 11 paired chromosomes were found on the heterotypic spindle. The division is somewhat irregular in some cases, but DAVIS (1911) has found a rather loose association of the chromosomes in the parental types. GEERTS (1911), however, found 7 bivalents and 7 univalents in the reduction division of the F_1 of *Oe. Lamarckiana* × *Oe. gigas*. The single chromosomes pass to either pole without dividing, usually 3 to one pole and 4 to the other. In the second division the univalents also divide irregularly.

The number of somatic chromosomes in species of Hieracium ranges from 18 to 42. In *H. excellens* (ROSENBERG 1917) with 42 chromosomes, 18 pairs of chromosomes are found on the heterotypic spindle in addition to 6 univalents. In the F_1 of *H. auricula* (18 chromosomes) × *H. aurantiacum* (36 somatic chromosomes), 9 bivalents were found with 8 or 9 univalents in the reduction division. The univalents divide irregularly. Similar chromosome behavior was found in other hybrids but often the number of univalents was found to vary even in the same cross.

TÄCKHOLM (1920) has found only paired chromosomes in the series 7, 14 and 21, in some Rosa species. Other species, especially those of the Canina section, have both bivalents and univalents at the time of reduction, usually 7 bivalents with 14, 21 or 28 univalents. The species which

have both bivalents and univalents in pollen reduction are thought to be hybrids which have been perpetuated for long periods of time by apomictical reproduction.

The behavior of the chromosomes in reduction divisions of species of Rosa has also been described in considerable detail by BLACKBURN and HARRISON (1921). In *R. Sabini* (*R. pimpinellifolia* × *R. sylvestris*) with 42 chromosomes, there are 14 bivalents and 14 univalents on the heterotypic spindle. The univalents lag behind in division but ultimately divide and pass to the poles. In the second reduction division the original bivalents pass rapidly to the poles and the daughter nuclei are reconstructed before the original singles reach the poles. Thus the major nuclei contain about 14 chromosomes. The univalent chromosomes form micronuclei and often a total of 8 nuclei are found which may be termed an "octad."

In one case in the above hybrid all of the chromosomes at the time of the homotypic division were on a single spindle. If development had been allowed to proceed the gametes would be able to produce a new plant octoploid in chromosome number.

In other Rosa hybrids BLACKBURN and HARRISON find a type of reduction similar to that found in *R. Sabini*, but involving 7 bivalents and 21 univalents or 14 bivalents and 21 univalents, etc. All roses showing such partial reduction are facultatively apomictical, due, according to the authors, to the stimulus of heterozygosis.

In Canna and Datura (BELLING 1921) the chromosome behavior in triploid individuals is quite different from that found in similar cases in Triticum, Rosa, Drosera, and Hieracium. In one clone of Canna the 27 chromosomes unite into 9 triads at reduction. The chromosomes of each triad pass at random, two to one pole and one to the other.

Among species hybrids in animals the chromosome behavior in F_1 reduction may vary greatly. FEDERLEY (1915) crossed two species of butterflies, each with 28 chromosomes. In the F_1 the chromosome number varied from 28 to 33 in spermatogensis, due to the varying number of single and double chromosomes on the plate. FEDERLEY believes that there is a negative correlation between the number of paired chromosomes and sterility in such cases. In another species cross FEDERLEY (1916) found little or no failure of the chromosomes to pair in reduction. In the F_1 of *Pygaera curtula* L. (29 chromosomes) with *P. anachoreta* F. (30 chromosomes) FEDERLEY (1913) found about 59 chromosomes in the reduction division, indicating that little or no pairing of chromosomes occurred. In a back-cross of the F_1 with *P. anachoreta* the chromosomes of

the same species paired leaving 29 single *curtula* chromosomes. The univalents divided equationally in both divisions, but the second division was often abnormal.

In general, triploid hybrids derived from species with different chromosome numbers have a similar type of chromosome behavior in the reduction divisions. Usually the number of bivalents is equal to the gametic number of chromosomes found in the parent with the smaller number, and the number of univalents is the difference between the chromosome numbers of the parental species. The bivalents divide normally while the univalents usually divide but once, equationally of course, and pass at random to either pole without dividing in one of the reduction divisions. Whether the single chromosomes divide in the first or second reduction division should make but little difference so far as the genetic results are concerned, providing that they divide but once. In case some or most of the univalents are not included in the functional pollen grains, as found in Rosa, the genetic behavior will be disturbed.

Chromosome behavior and sterility

The occurrence of a triploid chromosome number or the reduplication of a single chromosome is associated with more or less sterility. The relation of chromosome number and behavior to sterility is shown for Oenothera, Datura, and Triticum in table 6.

The percentage of apparently poor pollen grains as an indication of sterility is, of course, only an approximate measure, but for general purposes it is considered satisfactory. In Oenothera the species and hybrids having an additional chromosome or those which are triploid are much more sterile than the diploid or tetraploid types. Here, of course, the sterility may be disturbed also by the hybrid nature of most of the Oenotheras or due to balanced lethal factors. In Datura the reduplication of but a single chromosome results in some sterility, still greater sterility is found in the triploid individual, while the tetraploid species is as fertile as the diploid parental type. Tetraploid and hexaploid species of wheat are as fertile as diploid species. In pentaploid hybrids with 14 bivalents and 7 univalents the sterility is much less than in triploid hybrids with 7 bivalents and 7 univalents. The degree of sterility may, however, be greater than indicated by the appearance of the pollen grains. Sterility based on grains set per spikelet shows total sterility for the triploid hybrid and somewhat greater than 50 percent sterility in the pentaploid hybrid as compared with the parents. If we take into account the effect of hybrid vigor and compare the F_1 sterility

TABLE 6

Relation between chromosome number and sterility.

SPECIES	CHROMOSOME NUMBER	AVERAGE PERCENT OF POOR POLLEN
Oenothera (GATES 1915)		
Oe. gigas	28	54–72
Oe. Lamarckiana	14	42
Oe. lata rubricalyx × *rubricalyx* segregate	14	22
Oe. lata rubricalyx	14	33
Oe. semilata	15	77
Oe. lata-like	15	76
Oe. rubricalyx × *gigas*	21	81
Oe. gigas × *lata rubricalyx*	22	89
Datura (BLAKESLEE 1921)		
Normal	24	3
"New species"	48	3
Triploid	36	34
Trisomic (12 mutants)	25	8–21
Triticum (SAX 1921)		
Vulgare group	42	1
Emmer group	28	2
Einkorn group	14	1
Vulgare × Emmer F_1	35	12–22
Einkorn × Emmer F_1	21	98

with the grain set in fertile species crosses, the degree of sterility may be considered as about 60 to 70 percent in the pentaploid hybrids (see SAX 1921, table 4). The degree of sterility in pentaploid hybrids varies in different species crosses and the above is only a general statement of the facts. In Rosa there is also a high degree of correlation between chromosome duplication and sterility.

In all of the above cases the reduplication of both sets of parental chromosomes does not cause sterility or abnormal chromosome behavior. The triploid hybrid resulting from a cross of a diploid with a tetraploid species or a triploid individual resulting from other causes is characterized by abnormal chromosome behavior and sterility. In wheat, sterility is greater where the proportion of univalent to bivalent chromosomes is 1 : 1 than where the ratio is 1 : 2. In Oenothera, Datura, and in one case in Rosa sterility is associated with the reduplication of a single chromosome. The uniform relation between chromosome behavior and sterility in these cases indicates that similar factors are involved.

In some species hybrids the F_1 is completely sterile even though the parental chromosomes may be very similar. For instance *Crepis tectorum* is thought to have the same chromosome constitution as *C. virens*, but with one reduplicated pair (ROSENBERG 1919), but BABCOCK and COLLINS (1920) have found that a cross between the two species results in an F_1 individual which cannot even complete its vegetative development. Still more remarkable are the recent results of STURTEVANT (1921) with Drosophila. Seven mutant genes of *D. simulans* have been shown to be allelomorphic to mutant genes of *D. melanogaster*, but crosses of these species with a similar chromosome constitution results in sterile F_1 individuals. In other cases species with apparently similar chromosome constitution cannot even be crossed.

Sterility in wheat hybrids

A brief summary of the behavior of the F_2 generation of partially sterile hybrids will be of value in interpreting the correlation between chromosome behavior and sterility. In 1917, 84 seeds from an F_1 plant of Kubanka $\times$ Bluestem were planted in the greenhouse at BUSSEY INSTITUTION. Six seeds did not germinate; 18 germinated and grew but did not pass the rosette stage; 61 grew and formed heads, but 14 of these were completely sterile. Of the 47 plants which set grain only one or possibly 2 were as fertile as the parents. The average number of grains per spikelet for the 61 plants that headed was $.82 \pm .05$ as compared with an average of .56 for 30 F_1 plants and 2.45 for the parents. The correlation between sterility and height of the 61 plants that headed was $-.42 \pm .07$, indicating that the more sterile plants were poorly developed vegetatively.

The greater sterility of certain F_2 segregates as compared with the F_1 is shown also in a cross of *T. compactum* $\times$ *T. turgidum* grown by GAINES in 1921. The average grains per spikelet for the 293 F_2 plants that headed, was $.63 \pm .02$ as compared with $1.09 \pm .05$ grains per spikelet for the F_1. In the F_1 no plants were found in the sterility class .0—.2 grains per spikelet, while in the F_2 123 plants were in the lowest sterility class. The conditions under which the F_2 was grown were more favorable than for the F_1. Furthermore a large proportion,—probably more than half,—of the F_1 seed did not grow or did not produce plants which headed.

The relation of chromosome behavior to sterility in wheat hybrids

Let us now gather the facts that bear on the relation of chromosome behavior to sterility and to the origin and the relationships of the various

species of wheat. In general, sterility increases as the proportion of univalent chromosomes in the reduction division increases. In both triploid and pentaploid wheat hybrids the 7 univalents apparently pass at random to either pole in one of the reduction divisions. The degree of sterility may vary in pentaploid hybrids involving different parental species (HAYES, PARKER and KURTZWEIL 1920, SAX 1921). Many F_2 individuals may be less fertile than the F_1, but in the F_2 sterility is also associated to some extent with poor vegetative development. With the above cytological and genetic data it should be possible to suggest a cause of sterility in wheat hybrids.

If we assume that the tetraploid and hexaploid species are due simply to a reduplication of the chromosomes of a primary diploid species with only minor changes in the individual chromosomes, then the sterility must be due to quantitative relations between univalents and bivalents rather than any specific constitution of individual chromosomes. That such may be the case is suggested by the chromosome behavior in other genera where the univalents are known to be reduplicated chromosomes of a diploid species. With 7 univalent chromosomes assorting at random only 1 gamete in 64 would contain all or none of the univalents. If only gametes containing all or none of the univalents can develop and function, sterility would be almost complete. Such a relation of the chromosomes would explain practically all of the sterility found in triploid wheat hybrids, but it would not explain the greater fertility found in pentaploid wheat hybrids. Possibly the greater number of bivalents in pentaploid hybrids would permit normal development of gametes with an excess or deficiency of several univalents necessary for a diploid or triploid chromosome combination. If only gametes with 3 or 4 univalents, i. e., gametes with 17 or 18 chromosomes, failed to function, then somewhat more than half of the gametes would be sterile, which in general would agree with the degree of sterility in the F_1. Gametes with larger chromosome numbers might be expected to develop with a greater deviation from the normal gametic number than gametes with a small number of bivalents. In the F_2 individuals the number of univalents would never exceed the ratio found in the F_1 if homologous chromosomes always pair. If then sterility is due to the ratio of univalents to bivalents, the F_2 individuals would never be more sterile than the F_1.

On the other hand, it is probable that more than the mere numerical relations of the chromosomes is involved in the sterility of wheat hybrids. The great differences in morphological and physiological characters indicate that the chromosomes of the various species are unlike. The

different wheat groups have existed for long periods of time, apparently without the formation of intermediate types, so that the chromosome constitutions may differ greatly even though the polyploid species have originated by reduplication of the diploid set of a primary species. In the pentaploid F_1 hybrid the 14 chromosomes of the Emmer group presumably pair with the allelomorphs of the Vulgare group which they most nearly resemble. The 7 univalents would then perhaps contain factors primarily characteristic of the Vulgare species. If we assume that the members of the bivalent chromosomes can be interchanged in most cases without causing non-functional chromosome combinations, most of the sterility will be caused by the abnormal behavior of the univalent chromosomes. Gametes with 14 chromosomes, and with perhaps 1 or 2 additional univalents, would be fertile and would carry an excess of Emmer factors, while gametes with 21, 20 or 19 chromosomes would carry largely Vulgare factors. The assumption that gametes with 3 or 4 univalents do not develop is in accord with the cytological finding of KIHARA in F_3 segregates. The fertility increases as the chromosome number progresses from 38 to 42. Some 28-chromosome segregates were highly sterile. This latter case may be due to incompatible relations of the members of the 14 bivalent chromosomes. If therefore chromosome mixtures in the bivalents sometimes disturb gametic development,—although in most cases normal development is correlated with an increase or decrease in number of univalent chromosomes, with greatest fertility in 28- and 42-chromosome individuals,—then most of the data both on character transmission and on sterility can be explained. The union of similar gametes would produce segregates with a predominance of either Emmer or Vulgare characters. Intermediates would be formed by a union of the more extreme types. As a result there would be partial linkage of Emmer characters and of Vulgare characters, although pure parental types would rarely be recovered. A preliminary examination of the genetic data indicates that in the F_2 segregates of an Emmer-Vulgare cross many characters are partially linked. It would be possible only in rare cases therefore to combine the Emmer and Vulgare characters in a fertile homozygous individual. In order to explain why varieties or species with intermediate chromosome numbers such as 34 or 36 are not found, it is necessary to assume further that even the bivalent chromosomes cause sterility unless a complete set is present.

If a complete set of chromosomes is essential not only for gametic but also for somatic development, the greater sterility in F_2 could be explained on the ground that plants without a complete set of diploid

or triploid chromosomes vary directly in vegetative development with the completeness of chromosome constitution. In the F_1 two complete sets of chromosomes are present, so that somatic development is normal or is even increased through heterosis. In the F_2 the absence of certain chromosomes may result in various degrees of vegetative development, from plants that do not pass the rosette stage to plants which head out but are poorly developed. *In F_1 sterility is apparently due only to gametic chromosome combinations but in F_2 individuals a weak somatic development would prevent gamete formation although such formation might be possible on a normal plant. Thus the greater sterility in F_2 can be attributed, not to greater gametic sterility, but to a combination of somatic and gametic functions.* The fact that there is a rather high degree of negative correlation between sterility and size of plant indicates that much of the F_2 sterility is due to unfavorable vegetative development of the F_2 individuals.

The assumption that gametes are formed with a predominance of Emmer or of Vulgare factors in the F_1, would explain the absence of homozygous segregates combining the desirable characters of the two different groups. Many hybrids between members of the Vulgare and Emmer group have been made, but few if any of the segregates have contained the desired combinations of parental characters in a homozygous condition.

The above explanation would also agree with the hereditary behavior in F_2.[1] We would expect segregates to form in 3 classes, those with predominance of Emmer characters, those with predominance of Vulgare characters, and those with union of the two types. The latter class of segregates might be considerably reduced by sterility. In the F_2 we actually find considerable linkage of characters. In the F_2 of Amby × Kubanka the type of culm, whether solid or hollow, is partially correlated with length of glume, compactness of spikelet, carination of glume, glume color, pubescence, compactness of head, color of grain and texture of grain. It appears that the 17 characters described can be classed in 3 or 4 partially linked groups. Similar relations are found in other crosses. For instance in a cross of Marquis × Alaska with hollow and pithy

[1] The genetic results here summarized were obtained from an investigation in progress by Dr. GAINES and the writer. Five partially sterile hybrids were grown in the F_2 with a total of 714 individuals. The characters of the F_2 individuals were described and the data were punched on cards and analyzed with the aid of a sorting machine. In two crosses, involving descriptions of 17 characters, each character was correlated with every other character to determine the correlation between the various characters and the correlation of characters with sterility.

straw and hard and soft grain, respectively, there is a high degree of correlation between type of culm and hardness of grain ($r = .48 \pm .04$). It is possible, of course, that the high degree of association of parental characters found in these species crosses is due to chromosome linkage or in some cases to multiple effects of a single factor, but crosses within the Vulgare group have shown only a few linked characters. In either case the association of parental characters indicates the difficulty in combining the desirable characters of the Emmer and Vulgare groups.

The correlation between sterility, as indicated by grains per spikelet, and the number of heterozygous factors in F_2 individuals, should be relatively high if the F_1 gametes are predominantly Emmer or Vulgare in functional composition. Two classes of gametes, consisting largely of factors from either parent, would also be found if EAST'S (1915) hypothesis (B) is used to interpret the results. In either case the general method of gamete function is essentially the same, and in the F_2 the segregates resembling the parents should be relatively fertile while those intermediate like the F_1 should be relatively sterile. The correlation between sterility and number of heterozygous factors in an F_2 of *T. vulgare* × *T. turgidum* was found to be practically zero ($r = .03 \pm .06$). Similar results were obtained in other partially sterile wheat hybrids. If most of the 17 characters analyzed are dependent on factors in 2 or 3 chromosomes, little or no correlation would be expected between sterility and number of heterozygous factors.

Although many of the cytological and genetic facts are in accord with the sterility hypothesis presented, more work is necessary to put the chromosome and sterility relationships on a sound basis. Especially is more cytological work necessary in analyzing F_2 individuals. KIHARA (1921) has obtained chromosome counts of 8 F_2 plants in a partially sterile wheat cross and finds the chromosome number ranges from 31 to 42, but not in the frequency that would be expected. KIHARA believes that in the formation of an F_2 plant at least one gamete must have a complete set of either 14 or 21 chromosomes, but if all combinations of univalents and bivalents in the gametes are viable, as KIHARA apparently assumes, and if there is no selective fertilization, then only about 3 percent of the zygotes would develop. Moreover, if the sterility relationships depend on more than mere numerical ratios, and certain specific chromosome combinations cannot function, the degree of fertility will be greatly decreased. If, for instance, all 14 chromosomes of a 14-chromosome gamete must be from the Emmer parent, as KIHARA apparently assumes, then only one gamete in 16,384 would be functional in the F_1

plant. In any case, KIHARA's hypothesis is not in accord with either the cytological facts or with genetic results.

It appears that sterility in wheat hybrids is caused by other factors than those involved in partially sterile Nicotiana hybrids (EAST 1915). In wheat hybrids the abnormal behavior of chromosomes is associated with sterility, although incompatible chromosome combinations probably are factors as in the case of Nicotiana hybrids.

The origin of tetraploidy and hexaploidy in wheat species

The fact that the gametic chromosome number in the species of wheat are in multiples of 7 suggests that the tetraploid and hexaploid species are derived from a primary diploid species by chromosome reduplication. This view is also supported by the fact that several characters are dependent on 2 or 3 independent factors resulting in F_2 ratios of 15 : 1 and 63 : 1. It is also significant that the nearly related cereals have similar chromosome numbers. Rye has 7 haploid chromosomes and in the genus Avena, species are found with 7, 14 and 21 gametic chromosomes (KIHARA 1919). In other genera with polyploid species the tetraploid forms are in most cases known to have originated by chromosome duplication. In the wheat species and in certain other cases there is a striking correlation between chromosome number and cell size, which would indicate that the higher chromosome numbers are the result of duplication and not transverse fragmentation.

On the other hand there is evidence that does not support the view that tetraploidy and hexaploidy in wheat is actually due to chromosomal duplication. In cases where tetraploidy has occurred under experimental conditions the reduplicated sets of chromosomes assort at random in reduction which is not the case in tetraploid wheat species.

If the Emmer and Vulgare groups are the result of polyploidy, then, most if not all characters should be dependent on multiple factors. Of the characters which have been genetically investigated in wheat, 14 are apparently dependent on 1 factor, 4 characters behave as dihybrids, and only 1 character, red grain color, is clearly due to 3 independent factors in some cases. The latter character may also depend on only 1 or 2 factors in certain varieties. In wheat species, where the chromosomes of the polysomic sets assort in pairs, mutations could result in characters dependent on 1 or 2 factors; but in tetraploid species, where the chromosomes of a tetrasomic set assort at random, a single factor could not exist in the homozygous condition. It is possible that chromosomal duplication

occurred very early in the history of cultivated wheat and that in the course of time the individual chromosomes came to differ so that they no longer assorted at random within a reduplicated set.

Representations of all of the three groups of wheat can be traced back to prehistoric times (PERCIVAL 1921). Einkorn was probably one of the chief wheats grown in central Europe in the Neolithic period. Emmer was grown in Europe in prehistoric times and was grown in Egypt as early as 5400 B. C. It was the most important cereal in Egypt from the early ages until supplanted by Durum and Vulgare varieties in the Graeco-Roman period. Although representatives of the Vulgare wheat group were known to exist in Europe in prehistoric ages they were not the chief varieties grown until comparatively recent times. The great age of the three wheat groups may also explain why the groups differ so markedly in morphological characters even if they were originally derived from a single primary species by chromosome duplication. Although the species within each group overlap considerably, the differences between the three sterility groups are rather distinct. PERCIVAL has summarized the important characters which differentiate the Vulgare group from the Emmer group as follows: (1) Differences in arrangement of hairs on the leaf; (2) thin-walled, hollow culms; (3) a tough, non-disarticulating rachis; (4) absence of keel on the lower part of the glume in most cases; and (5) the comparatively short awns of the fully bearded varieties and the occurrence of beardless and semi-bearded varieties. The greatest difference is, of course, the high quality of the gluten in most of the Vulgare varieties. No variety of the Emmer group contains gluten of the quality necessary for the production of light spongy bread. The species of the Emmer group are, in general, best adapted to a hot dry climate, and because of susceptibility to cold weather, they are in few cases sown in the fall in the temperate zone.

Many of the characters which distinguish the Vulgare from the Emmer group are found in *T. aegilops ovata* or *T. aegilops cylindrica* and accordingly PERCIVAL has concluded that the Vulgare group is a hybrid race resulting from an early cross or crosses of members of the Emmer group and *T. aegilops*. The hybrids of the present species of the Emmer group or even *T. dicoccoides* with *T. aegilops* are, however, nearly or quite sterile in the F_1.

Chromosome number and adaptability in wheat species

The characters of the Vulgare group are subject to very wide variation and the great number of varieties and intermediate forms are believed by

PERCIVAL to be due to their hybrid origin. The great variability and adaptability of the Vulgare wheats may, however, be due to other causes. EAST (1915) suggested that variability of a species would be correlated with the chromosome number and DORSEY in 1916 suggested that the adaptability of a species might be correlated with chromosome number. With an increase of chromosome number the number of factorial combinations would increase, thus resulting in a greater range of adaptation. There is certainly a high degree of correlation between chromosome number and adaptability in the species of wheat. The number and distribution of the varieties of the cultivated species of wheat are shown in table 7.

TABLE 7

Number and distribution of varieties of the Einkorn, Emmer and Vulgare groups. (*Data from* PERCIVAL 1921.)

	T. monococcum	*T. dicoccum*	*T. durum*	*T. polonicum*	*T. turgidum*	*T. pyramidale*	*T. vulgare*	*T. compactum*	*T. sphaerococcum*	*T. Spelta*
Number of "varieties"	3	40	22	23	27	5	26	20	6	12
Groups		Emmer					Vulgare			
Haploid chromosome number	7	14					21			
Distribution of "forms"										
S. E. Europe, S. W. Asia	*	10					9			
Southern Europe	*	77					42			
Russia		7					12			
Central and N. Europe		27					102			
England		13					91			
India		2					4			
Australia and New Zealand		3					63			
South Africa		4					23			
Japan and China							11			
North America		7					109			
South America		1					7			
Total		151					536			

*Species of Einkorn grown but no cultivated "forms" described.

PERCIVAL (1921) recognizes only two wheat species, *T. aegilopoides* and *T. dicoccoides*, and suggests that the other types might be classed as

"cultivated species." Under the term "forms" PERCIVAL classes what are commonly known as varieties, such as Marquis, Bluestem, Kubanka, etc. It will be seen in table 7 that the number of the varieties is greatest in the Emmer group, but that the Vulgare group contains almost four times as many "forms." The distribution of the different groups is also significant. The members of the Einkorn and Emmer groups are found in greatest numbers in the regions where wheat originated. In general the region has a warm dry climate. The members of the Emmer group are comparatively rare in Australia, England, South Africa, Japan and North America. Members of the Vulgare group are found all over the world wherever wheat is grown and under diverse climatic conditions. Although the Vulgare group is more variable and adapted to a greater range of conditions they are not always the highest yielders. Certain varieties of *T. turgidum* are the most productive of all wheats, and under certain conditions varieties of *T. durum* will outyield the Vulgare varieties. The correlation between chromosome number and adaptability in wheat species may not depend on a causal relationship. The Vulgare group may be more highly selected and more widely distributed because it is the only wheat suitable for making light bread. The greater variation and adaptability would also be expected if the Vulgare group is a vast hybrid race as PERCIVAL has suggested. A study of chromosome number in relation to variations and adaptability in polyploid species under natural conditions would be of interest.

The value of tetraploidy

Since tetraploidy usually results in increased size of plant tissues and possibly permits greater adaptability, the development of tetraploid species may be of value. WINKLER (1916) has obtained tetraploid forms of tomatoes and nightshade in connection with his work on graft hybrids. The tetraploid forms were larger than diploid forms but unfortunately they were sterile. A number of investigators have been able to induce changes in the chromosome number of somatic cells by treatment with various reagents (SAKAMURA 1920) but it appears to be questionable if such changes can be maintained and established in later generations. CASTLE (1921) has suggested that the French prune mutation described by SHAMEL (1919) is the result of tetraploidy. It is not improbable that the best cases of bud mutations involving increased productivity (if such mutations actually occur) will be found to be associated with tetraploidy or chromosome duplication.

DESCRIPTION OF PLATES

Preparations from pollen mother cells at the time of the reduction divisions. The drawings were made with the aid of a camera lucida. All figures were drawn from single sections. Magnification 750 diameters. No reduction. The reproduction of these drawings has been made possible by financial assistance from BUSSEY INSTITUTION.

PLATE 1

Triticum monococcum

FIGURE 1.—The 7 paired chromosomes at diakinesis.
FIGURE 2.—Metaphase, polar view. Heterotypic division.
FIGURE 3.—Metaphase, side view.
FIGURE 4.—Late anaphase, 7 chromosomes at each pole.
FIGURE 5.—Polar view of late anaphase showing the 7 chromosomes split for the homoeotypic division.
FIGURE 6.—Telophase of the homoeotypic division.

The Emmer group

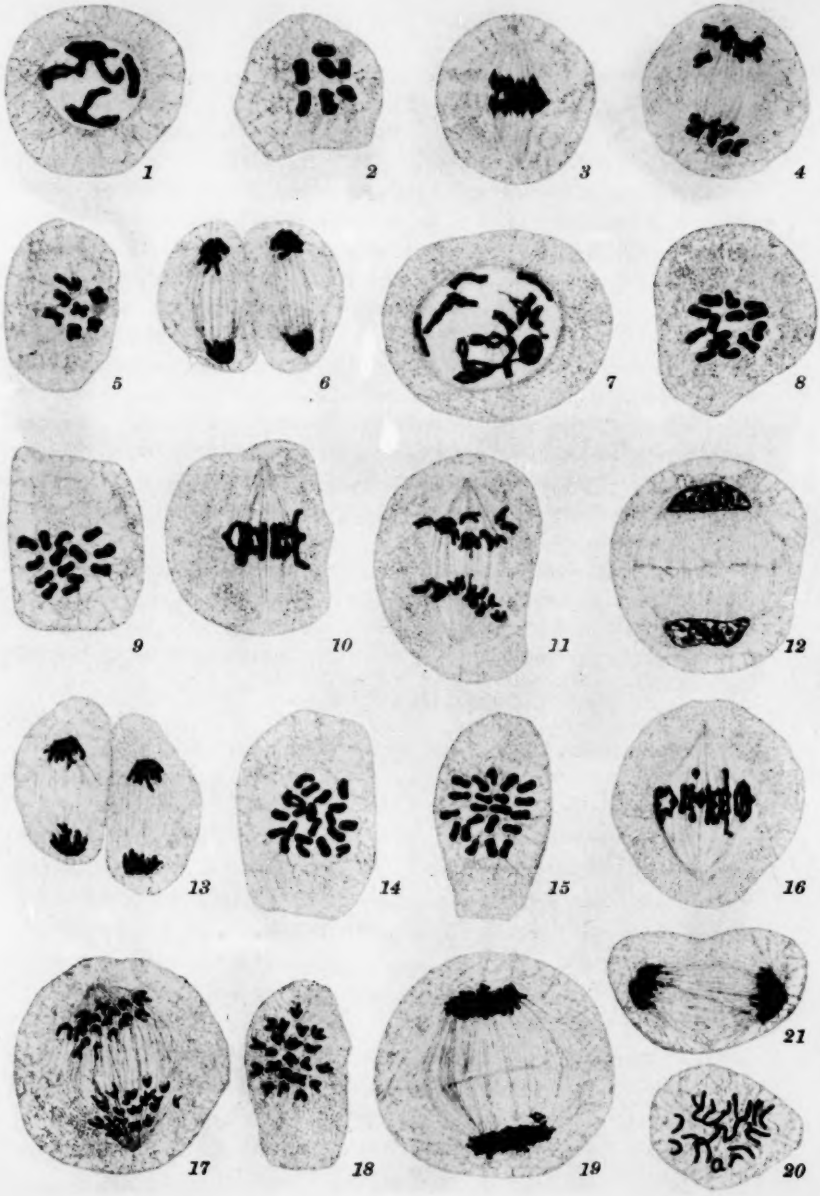
FIGURE 7.—Diakinesis. 14 pairs of chromosomes. *T. durum.*
FIGURE 8.—Metaphase, polar view. 14 chromosomes.

T. polonicum

FIGURE 9.—Metaphase, polar view. *T. durum.*
FIGURE 10.—Metaphase, side view. *T. polonicum.*
FIGURE 11.—Anaphase of heterotypic division. *T. polonicum.*
FIGURE 12.—Interkinesis. Resting nuclei. *T. polonicum.*
FIGURE 13.—Telophase of homoeotypic division. *T. durum.*

The Vulgare group

FIGURE 14.—Metaphase, polar view. 21 chromosomes. *T. Spelta.*
FIGURE 15.—Metaphase, polar view. 21 chromosomes. *T. vulgare.* (Preston)
FIGURE 16.—Metaphase, side view. *T. vulgare.* (Preston)
FIGURE 17.—Late anaphase of heterotypic division, side view. *T. vulgare.* (Preston)
FIGURE 18.—Late anaphase, polar view. *T. vulgare.* (Preston)
FIGURE 19.—Telophase. *T. vulgare.* (Marquis)
FIGURE 20.—Metaphase. Homoeotypic division, polar view. *T. vulgare.* (Amby)
FIGURE 21.—Telophase, homoeotypic division. *T. vulgare.* (Amby)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The value of polyploidy may have certain limitations. As TUPPER and BARTLETT (1918) have suggested, a few doublings in chromosome number would increase the size of the cell so that respiration and nutrition would be retarded. In Crepis and Chrysanthemum, however, the chromosome number has apparently been duplicated many times without disastrous results. MULLER (1918) believes that tetraploidy would hinder evolution because recessive mutants could rarely manifest themselves. If recessive factors have some effect in the presence of dominant factors, which is frequently or perhaps usually the case, then increased variability would result even if the pure recessive could rarely be isolated.

There has been considerable discussion as to the origin of tetraploid species especially in Oenothera. GATES (1915) argues that *Oe. gigas* must have originated by a doubling of chromosomes at an early stage in somatic development of a diploid species, because of the rare occurrence of diploid gametes. This interpretation is undoubtedly the most reasonable in cases where tetraploid individuals have suddenly originated from a diploid species. If a diploid gamete united with a normal haploid gamete and the chromosomes in the trisomic sets assorted at random 25 percent of the F_2 segregates would be tetraploid. The occasional occurrence of diploid gametes has been observed in several diploid species and would afford an opportunity for the formation of tetraploid species although the latter would originate from a triploid individual and not directly from the original diploid species.

Pollen-grain variability

The pollen of F_1 plants of species hybrids is much more variable than the pollen of pure species.

The remarkable relation between heterosis or degree of germinal mixture and variability of pollen grains is especially interesting because the pollen grains belong to the gametophytic generation. In most cases recorded the characters of the pollen grain are determined by the mother plant. BATESON (1909) has found that the shape and color of pollen in the sweet pea behave as sporophytic characters. EAST (1916) has found a similar behavior of pollen in Nicotiana and also finds that self-sterility behaves as a sporophytic character (EAST 1919). On the other hand BELLING (1914) has found segregation of normal and aborted pollen grains in semi-sterile F_1 hybrids, and PARNELL (1921) finds segregation of equal numbers of starchy and glutinous pollen grains in an F_1 rice hybrid. The occurrence of the starchy and glutinous pollen grains

DESCRIPTION OF PLATE 2

T. monococcum (7-chromosome gametes) × *T. turgidum* (14-chromosome gametes)

FIGURE 22.—Metaphase of heterotypic division with 7 bivalents (1 divided) and 7 univalents at the poles.

FIGURE 23.—Late anaphase with approximately 10 chromosomes at either pole due to the division of the bivalents and the random assortment of the univalents without dividing.

FIGURE 24.—Early telophase. Split chromosomes, originally members of the bivalent chromosomes, just reaching the poles.

FIGURE 25.—Telophase. No lagging chromosomes.

FIGURE 26.—Anaphase of homoeotypic division. Vulgare group (21-chromosome gametes) × Emmer group (14-chromosome gametes), F_1 plants.

FIGURE 27.—Metaphase, polar view, of homoeotypic division with about 10 chromosomes in each figure.

FIGURE 28.—Metaphase of heterotypic division, polar view. Fourteen bivalents and 7 univalents. Amby × Kubanka.

FIGURE 29.—Metaphase showing bivalents and univalents. Bluestem × Alaska.

FIGURE 30.—Metaphase of heterotypic division showing irregularly distributed univalents. Note the attachment of the spindle fibers and apparent tension of the chromosomes. Amby × Kubanka.

FIGURE 31.—The bivalents have divided leaving the 7 univalents and apparently several additional unpaired chromosomes on the equatorial plate. Amby × Kubanka.

FIGURE 32.—The 14 bivalents have divided and reached the poles while the 7 univalents are dividing equationally. Amby × Kubanka.

FIGURE 33.—A similar stage in Bluestem × Kubanka.

FIGURE 34.—A similar stage in Bluestem × Kubanka.

FIGURE 35.—The 7 univalents have divided and have nearly reached the poles. Bluestem × Alaska.

FIGURE 36.—Homoeotypic division showing univalents which do not divide but pass at random to either pole and join the original 14 bivalents.

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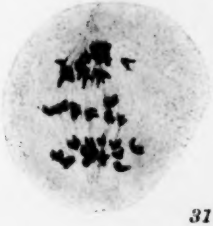
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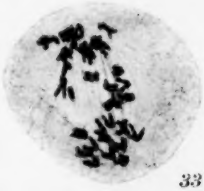
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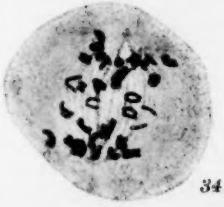
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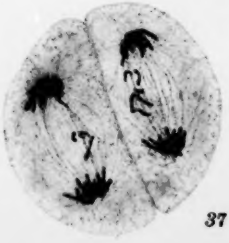
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is undoubtedly due to the effect of the segregated factors. In the wheat hybrids the factors for growth apparently segregate into various proportions of maternal and paternal factors in the F_1 and the various combinations of these factors may cause increasd variation in size of pollen grains, ranging from completely aborted grains to those much larger than normal. The increased variability is due here to combinations of non-homologous chromosomes acting in the gametophytic generation and to differences in chromosome number. In cases where the gametophytic characters are controlled by the sporophyte the characters may be those primarily caused by the sporophyte, such as pollen-grain shape and possibly color. In other cases certain characters, such as growth and starch-formation, may be controlled by the gametophytic chromosomes at an early stage in the development of the gametophyte, while perhaps other characters cannot be brought into expression until the necessary development of the organism has been attained.

SUMMARY

The chromosome number and behavior has been determined for the cultural species of Triticum and for certain partially sterile hybrids.

The gametic chromosome number is 7 for *T. monococcum*; 14 for the Emmer group, consisting of *T. dicoccum*, *T. durum*, *T. polonicum*, and *T. turgidum;* and 21 for the Vulgare group, consisting of *T. vulgare*, *T. compactum* and *T. Spelta*. Rye (*Secale cereale*) has 7 gametic chromosomes.

In the F_1 hybrid of *T. monococcum* × *T. turgidum* 7 chromosomes are contributed by one parent and 14 by the other parent. In the heterotypic division of the pollen mother cells there are 7 bivalents and 7 single chromosomes. The 7 bivalents divide normally, but the 7 univalents pass at random to either pole without dividing. In the homoeotypic division there are usually about 10 or 11 chromosomes which apparently divide normally in most cases. Tetrads and one-nucleate pollen grains appear to be normal, but very few normal mature pollen grains are formed.

In F_1 hybrids between members of the Emmer group and members of the Vulgare group, 14 chromosomes are contributed by one parent and 21 by the other parent. In the first meiotic division there are 14 bivalent and 7 univalent chromosomes. The bivalents divide normally, but the univalents do not become oriented on the equatorial plate until the bivalents have divided. The 7 lagging univalents divide equationally and 7 chromosomes pass to each pole. In the homoeotypic division the

DESCRIPTION OF PLATE 3

Micro-photographs of chromosomes in the reduction divisions of the pollen mother cells in wheat species, rye, and wheat hybrids. Photographs not retouched.

FIGURE 37.—Late anaphase showing the 7 chromosomes in Einkorn.

FIGURE 38.—Late anaphase, side view. Einkorn.

FIGURE 39.—Late anaphase with 14 chromosomes at one pole. Polish.

FIGURE 40.—Metaphase, polar view. 21 chromosomes. Preston.

FIGURE 41 A, B.—Diakinesis in rye, showing the 7 pairs of twisted chromosomes.

FIGURE 42.—Metaphase showing univalents and bivalents in (Amby × Kubanka) F_1.

FIGURE 43.—Bivalent chromosomes have divided and reached the poles while the split univalents are on the heterotypic plate. (Amby × Kubanka) F_1.

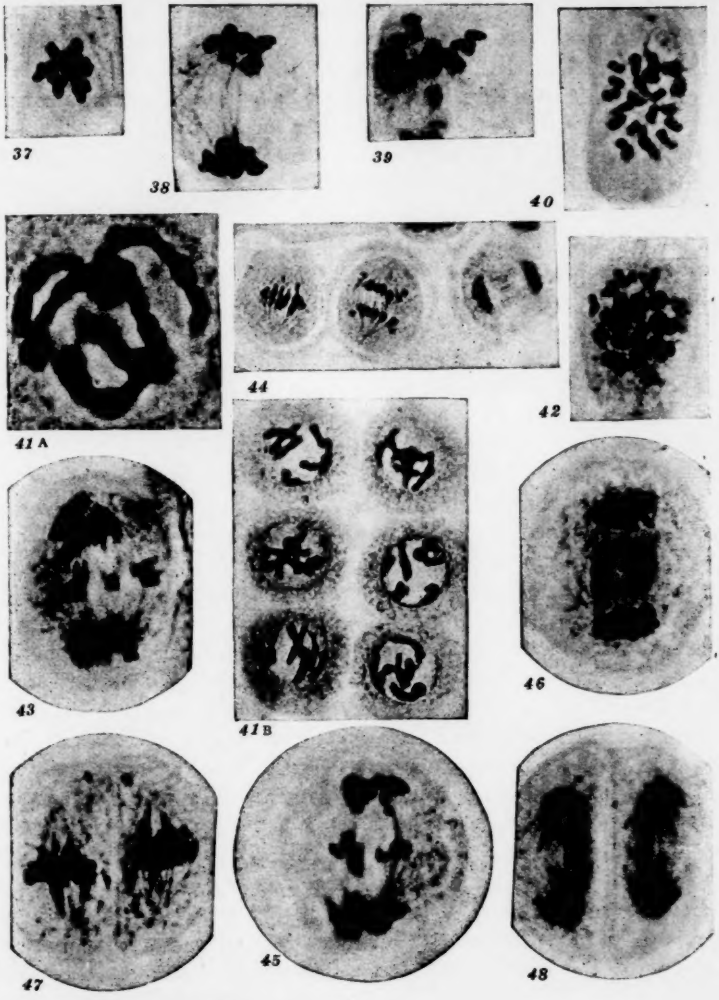
FIGURE 44.—Metaphase, anaphase, and telophase in 3 adjacent pollen mother cells in an anther of Preston.

FIGURE 45.—Same as figure 43.

FIGURE 46.—Telophase, no lagging chromosomes. (Amby × Kubanka) F_1.

FIGURE 47.—Metaphase, side view of the homoeotypic division showing several irregularly distributed chromosomes. (Amby × Kubanka) F_1.

FIGURE 48.—Homoeotypic division showing lagging chromosomes. Same as figure 36. Amby × Kubanka) F_1.



J. W. B. and K. S. photo.

original members of the bivalents divide normally, but the remaining 7 chromosomes pass at random to either pole without dividing. As a result the chromosome number of the microspores varies from 14 to 21. The tetrads and one-nucleate pollen grains appear to be normal, but in later stages about 20 percent of the pollen grains are obviously imperfect and undoubtedly a larger percentage is non-functional.

The size of the pollen grains is closely correlated with the chromosome number in the various species of wheat.

The pollen grains of fertile species hybrids are more variable than the pollen grains of the parental species due to various degrees of compatibility of the combinations of non-homologous chromosomes in the gametophytic generation. In partially sterile hybrids where the parental species differ in chromosome number, the pollen grains are extremely variable, due to difference in chromosome number and to more or less compatible chromosome combinations.

The sterility in the hybrids described can be accounted for on a hypothesis involving, (1) the numerical or unbalanced relations of the chromosomes resulting from the irregular meiotic divisions, and (2) the specific interrelations of the parental chromosomes. In the numerical relations the development of gametes varies as the chromosome number approaches the normal gametic number (7, 14 or 21). It is assumed that the greater the gametic chromosome number the greater can be the deviation from the normal number. The specific relations of the gametic chromosomes will depend on the extent that chromosomes from one parent can be substituted for those of the other parent. Gametic perfection will vary as the chromosome constitution approaches that of the parental forms. The 7 univalents in the Emmer-Vulgare F_1 hybrids presumably carry most of the factors which differentiate the Vulgare characters from the Emmer characters.

This hypothesis will explain (1) the differences in sterility of the various species hybrids, (2) the partial association of the original parental characters in the F_2 segregates, (3) the absence of varieties or species with intermediate chromosome numbers, and (4) the difficulty in obtaining homozygous segregates combining the desirable characters of the parental species in partially sterile wheat hybrids.

In all cases the F_1 plants are unusually vigorous and sterility is not due to poor vegetative development, but is caused by the formation of non-functional gametes. Sterility in F_2 segregates may be greater than in F_1 individuals due, not to greater gametic sterility *per se*, but to a combination of weak somatic development and gametic sterility.

The evidence for and against the occurrence of chromosome duplication in wheat species is presented and discussed.

There is a high degree of correlation between chromosome number and adaptability in the wheat species, but the relation may not be a causal one.

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STERILITY IN WHEAT HYBRIDS. III. ENDOSPERM DEVELOPMENT AND F_2 STERILITY

KARL SAX

Maine Agricultural Experiment Station, Orono, Maine

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Crosses of wheat species with different chromosome numbers result in small or wrinkled seeds. These seeds consist of the F_1 endosperm and the embryo of the F_1 plant. Although the F_1 endosperm is usually poorly developed, the F_1 plant is even more vigorous than the parents. The F_1 plants are partially sterile and bear grains (F_2 endosperms) which vary greatly in size. Since small wrinkled grains are characteristic of partially sterile hybrids the small wrinkled grains borne on the F_1 plant might be expected to produce partially sterile F_2 plants, while the large plump grains would produce relatively fertile F_2 individuals.

It is well known that wide species crosses in wheat result in partially sterile F_1 plants and that in F_2 all degrees of sterility are found, ranging from plants which never pass the rosette stage, to those quite as fertile as the parents. A study of sterility in view of the chromosome relationships should be of value.

The parental varieties of wheat used were *Triticum durum* Desf. (Kubanka) and *T. vulgare* Vill. (Pacific Coast Bluestem). The crosses were made in 1916 and the F_1 was grown at BUSSEY INSTITUTION in 1917. The F_2 was grown in the greenhouse in 1917–1918.

WEIGHT OF SEEDS OF PARENTS AND HYBRIDS AND F_1 STERILITY

The degree of sterility, as indicated by the grains set per spikelet, and weight of grains of parents and the F_1 hybrids are shown in table 1. The F_1 plants are about one-fourth as fertile as the parents, although they are more vigorous vegetatively as indicated by the greater number of heads per plant. There is little difference in the fertility of the reciprocal hybrids. For the 30 F_1 plants the average number of grains per spikelet was found to be $0.57 \pm .03$ with a standard deviation of $0.25 \pm .02$. The sterility of the F_1 plants varied from .07 to 1.00 grain per spikelet. It appears probable that with larger numbers some F_1 individuals would

TABLE 1

Weight of grain and sterility in parents and hybrids.

NO. OF PLANTS	NO. OF HEADS	NO. OF SPIKELETS	NO. OF GRAINS	GRAINS PER SPIKELET	WEIGHT OF GRAINS IN 5-MG UNITS															NUMBER	MEAN	STANDARD DEVIATION
					2.5-7.5-	7.5-	12.5-	17.5-	22.5-	27.5-	32.5-	37.5-	42.5-	47.5-	52.5-	57.5-	62.5-	67.5-	72.5-77.5-			
Kubanka																						
6	9	144	386	2.68					1	8	25	30	45	55	89	82	20	1		356	48.9±.3	8.9±.2
Bluestem																						
7	23	354	789	2.23				1	2	14	27	51	115	123	100	24	2			458	45.2±.2	7.4±.2
(Kubanka × Bluestem)F_1 endosperm																						
							2	4	7	6	4	1								24	24.4±.9	6.4±.6
(Kubanka × Bluestem)F_1 (F_2 endosperm)																						
15	152	2323	1413	.61	4	19	31	50	106	124	138	154	183	161	175	121	103	33	11	1413	41.4±.3	14.5±.2
(Bluestem × Kubanka)F_1 (F_2 endosperm)																						
15	131	1932	990	.51	9	22	34	50	77	109	115	123	114	110	95	70	37	19	6	990	38.1±.3	14.7±.2

be totally sterile, although the percentage of such plants would be small. The variation in sterility of the F_1 plants is apparently not due to differences in vegetative development, because the correlation between sterility, as indicated by the number of grains set per spikelet, and vegetative vigor, as indicated by the number of heads per plant, is practically zero ($r = -.08 \pm .12$).

Kubanka has somewhat larger seeds than Bluestem, but the variability of grain weight does not differ greatly although the difference is statistically significant. The grains resulting from the immediate cross (F_1 endosperm) are but little more than half as heavy as the grains of the parents and are no more variable. The grains borne by the F_1 plants[1] (F_2 endosperm) are extremely variable, with a standard deviation of nearly twice that of the parental grain weight. The average grain weight of the F_1 plants is greater when Kubanka is used as the female parent, but the difference, although statistically significant, may depend on environmental and not genetic factors.

STERILITY IN THE F_2 GENERATION

The seed from an F_1 plant of Kubanka × Bluestem was planted in the greenhouse under very uniform and favorable conditions. The F_1 plant selected was representative of all F_1 plants, both in vegetative development and sterility. Of the 84 seeds planted 6 failed to germinate, 78 seeds germinated but of these only 61 produced heads and only 47 produced grain. In the entire F_2 only 1 or perhaps 2 plants were as fertile as the parents. The descriptions of the F_1 grain (F_2 endosperm) and the resulting F_2 plants are given in table 2.

The sterility in F_2 ranged from plants which were totally sterile to one which set 2.66 grains per spikelet. The mean sterility of the 61 plants that headed was found to be .83 with a standard deviation of .64. Thus in the F_2 a larger proportion of plants is totally sterile than in the F_1. Moreover, many F_2 plants fail to develop normally and a large percentage fails to produce heads. Under field conditions probably half of the F_1 grain fails to produce viable F_2 plants, and under unfavorable climatic conditions nearly all F_1 grains fail to develop, even though standard varieties may show more than 50 percent germination under the same conditions. Much of the extreme sterility in F_2 is undoubtedly due to

[1] The mean weight and variability of seeds of parents and F_1 plants were relatively uniform, so all individuals of each class were grouped together. The variability in seed weight is not due to differences in average seed weight of individual plants.

TABLE 2

Kubanka × Bluestem—F_1 and F_2.
(*Greenhouse* 1917.)

F_1			F_2				F_1			F_2			
Grain No.	Weight in mg*	Wrinkled or plump	Height of plant in cm	No. of spikelets	No. of grains	Grains per spikelet	Grain No.	Weight in mg	Wrinkled or plump	Height of plant in cm	No. of spikelets	No. of grains	Grains per spikelet
1	15	W	127	120	156	1.30	43	45	P	96	54	62	1.15
2	20	W					44	45	P	128	80	20	.25
3	20	W					45	45	P	128	60	45	.75
4	20	P					46	45	P	117	+	0	.00
5	25	W	132	106	142	1.34	47	45	P	*9*			
6	25	W	131	90	111	1.23	48	45	P	137	148	213	1.44
7	25	W	118	72	78	1.10	49	50	W	145	66	21	.32
8	30	W	123	68	23	.34	50	50	W	109	+	0	.00
9	30	W					51	50	W	128	+	0	.00
10	30	W	124	100	200	2.00	52	50	W	54	+	0	.00
11	30	P	136	115	58	.50	53	50	W	140	100	41	.41
12	30	P					54	50	W	*14*			
13	35	W	119	92	127	1.38	55	50	W	*13*			
14	35	W	115	124	177	1.42	56	50	P	107	88	16	.18
15	35	W	130	74	6	.08	57	50	P	80			
16	35	W	128	47	125	2.66	58	50	P	30			
17	35	W	130	150	68	.45	59	50	P	115	+	0	.00
18	35	P	105	74	10	.14	60	50	P	40			
19	40	W	126	116	152	1.31	61	50	P	129	188	391	1.81
20	40	W	136	102	96	.94	62	50	P	*13*			
21	40	W	*10*				63	55	W	*14*			
22	40	W	122	122	185	1.52	64	55	W	115	151	253	1.70
23	40	W	35				65	55	W	142	102	37	.37
24	40	W	*10*				66	55	W	114	86	118	1.37
25	40	W	110	60	77	1.28	67	55	W	*14*			
26	40	W	105	80	57	.71	68	55	P	124	138	180	1.30
27	40	W	40				69	55	P	105	100	131	1.31
28	40	W	*11*				70	55	P	87	+	0	.00
29	40	W					71	55	P	147	36	52	1.44
30	40	W	127	130	183	1.41	72	55	P	145	192	306	1.60
31	40	P	106	112	73	.65	73	55	P	50	+	0	.00
32	40	P	*7*				74	60	W	130	94	111	1.18
33	40	P	100	+	0	.00	75	60	W	115	+	0	.00
34	40	P	117	80	15	.19	76	60	P	60			
35	40	P	60	+	0	.00	77	60	P	135	126	216	1.71
36	40	P	40				78	60	P	86	+	0	.00
37	45	W	132	70	50	.70	79	60	P	153	104	136	1.31
38	45	W	121	68	78	1.14	80	65	W	90	+	0	.00
39	45	W	100	130	59	.45	81	65	W	115	100	167	1.67
40	45	W	137	126	67	.53	82	65	W	155	34	10	.30
41	45	W	108	100	29	.29	83	65	P	61	+	0	.00
42	45	P	130	84	138	1.64	84	70	W	63	+	0	.00

poor vegetative development of certain plants. Such a relation is indicated by the relatively high correlation between sterility and height of the 61 F_2 plants which headed ($r = .42 \pm .07$). Among the 47 plants which set grain the high sterility of certain individuals does not seem to be due to poor vegetative development, since there is no significant correlation between height and sterility of the 47 F_2 plants ($r = .04 \pm .10$).

The 84 F_1 grains were extremely variable in weight and were also variable in shape,—whether wrinkled or plump. In table 2 the F_1 grains are arranged in order of weight and arbitrarily classified as wrinkled or plump. The average weight of the wrinkled grains was found to be but little less than the weight of the plump grains. The correlation between weight and plumpness of grain was found to be rather low ($r = .23$). The correlation was determined by a method suggested by PEARSON (1909).

Among the F_1 seeds which failed to germinate, a majority are in the lower weight classes, but among the 78 plants which grew there is little or no correlation between weight of F_1 grains and height of the resulting F_2 plant ($r = -.10 \pm .05$). The correlation is not greatly increased by using only the 61 F_2 plants which headed ($r = -.20 \pm .08$.) The size of the F_1 grain gives little indication of the probable size of the F_2 plant. The plumpness of F_1 grains has little or no effect on the size of F_2 plants. For the 78 F_2 plants the correlation between wrinkled or plump F_1 grain and height of F_2 plants was found to be only .10, and for the 61 plants which headed, $r = .10$.

A similar correlation was found between F_1 grain weight and F_2 sterility. For the 47 F_2 plants that headed, the correlation between F_1 grain weight and F_2 sterility was $.03 \pm .10$, and for all 78 plants, $r = -.19 \pm .08$. The correlation between wrinkled or plump F_1 grains and F_2 sterility was found to be .24 for the 61 F_2 plants which headed. Although small wrinkled grains are characteristic of partially sterile hybrids there is little or no correlation between F_1 grain weight or shape and the height or sterility of the resulting F_2 plants.

DISCUSSION AND SUMMARY

In a cross of Kubanka × Bluestem a male gamete with 21 chromosomes unites with an egg cell containing 14 chromosomes. In the endosperm there are 28 chromosomes of maternal origin and 21 chromosomes of paternal origin while in the reciprocal cross 42 chromosomes are contributed by the polar nuclei and only 14 by the sperm nucleus. Such unbalanced conditions of the chromosome sets might be expected to

result in abnormal endosperm development, although in pure species the triploid condition of the endosperm does not result in abnormal development, unless endosperm formation itself is considered abnormal. Endosperm formation is not due simply to the triploid condition, however, because triploidy is found in the vegetative cycle of a number of plants.

The greatly increased variability of the F_1 grain (F_2 endosperm) can be attributed to differences in chromosome number, to recombinations of factors for growth, and to more or less compatible chromosome combinations. Although the maximum mixture of parental chromosomes is found in the F_1 endosperm the F_2 endosperms may in many cases be significantly smaller than F_1 endosperms, due to inharmonious chromosome relations.

Since poorly developed F_1 endosperm is associated with sterility and unusual vegetative vigor of the F_1 plant, a high degree of correlation would be expected between F_2 endosperm development and sterility and vegetative development of F_2 plants. An analysis of the data shows, however, that there is little or no correlation between F_2 endosperm development and F_2 sterility or vegetative development. Apparently the results of the peculiar chromosome relationships in endosperm formation do not indicate the nature of the chromosome relations of the accompanying embryo. This relation may be due to the greater opportunity for an unbalanced condition of maternal and paternal chromosomes in the endosperm.

The increased sterility in F_2 individuals as compared with the F_1, and especially the weak somatic development of many plants, may be attributed to chromosome combinations incompatible for vegetative development. The chromosome compatibility may depend on numerical or balanced relation of the chromosomes or on specific chromosome relationships. In F_1 plants two complete sets of chromosomes are present and the F_1 plant is unusually vigorous even though it is partially sterile. In F_2 individuals a complete set of chromosomes of either parent would rarely be found and the perfection of somatic development would be expected to vary with the completeness of the parental sets of chromosomes. Thus in F_2 many individuals are completely sterile because of weak vegetative development as well as gametic sterility.

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INHERITANCE OF ZIGZAG CULMS IN MAIZE

WILLIAM H. EYSTER

University of Missouri, Columbia, Missouri

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TABLE OF CONTENTS

INTRODUCTION 559
Description of zigzag culms 560
Terminology 560
Inheritance of zigzag culms 560
Behavior in the F_1 and F_2 generations 560
F_1 plants back-crossed with zigzag plants 562
Further tests of the back-crossed plants 562
Linkage between the factor pairs Z_g z_g and G_s g_s 565
SUMMARY 566
LITERATURE CITED 567

INTRODUCTION

Maize plants with zigzag culms were first observed by Dr. R. A. EMERSON in a number of fourth-generation families from a cross between Tom Thumb pop corn and a Missouri dent corn. The appearance of plants with zigzag culms was probably due to a recombination of factors from the plants in the original cross. In the summer of 1917 Dr. EMERSON turned over to me for further study a strain of maize breeding true for zigzag culms. In a preliminary paper (EYSTER 1920) it was suggested that two factors are concerned in the production of zigzag culms in maize. When both factor pairs are recessive the culms of the main plant and tillers are zigzag, but the dominant allelomorph of either pair is sufficient to produce normal culms. Sufficient data have since been accumulated, it is thought, to establish this explanation. Much of the experimental work reported here was done at CORNELL UNIVERSITY. I am indebted to that institution and to DR. EMERSON, especially, for placing at my disposal facilities for the work. The remainder was done at the MISSOURI AGRICULTURAL EXPERIMENT STATION, as a project of the Department of Field Crops, UNIVERSITY OF MISSOURI. I am also indebted to L. A. EYSTER for taking some of the notes.

DESCRIPTION OF ZIGZAG CULMS

EMERSON (1912) described maize plants with zigzag culms in connection with a number of other recessive abnormalities in maize which he was studying at that time. The writer (EYSTER 1920) more recently published a series of illustrations to show the nature of zigzag culms and the variation in its expression.

Zigzag culms come into expression at about the time the tassel and ear shoots make their appearance. The first evidence is an apparent flattening and widening of the culm. This is due to the spreading apart of the over-lapping leaf sheaths by the crooks in the culm. In extreme cases the sheaths are pushed aside so far that they no longer clasp the culm and therefore give no mechanical support to the rapidly elongating culm.

When the leaf sheaths are removed it is seen that some of the internodes, varying from two or three in some plants to as many as ten or twelve in other plants, are shortened, thickened and crooked. It is usually the internodes in the ear-shoot region that are so affected. Sometimes the abnormality appears in more than one region of the culm with apparently normal internodes between the affected regions. Plants in which a large number of internodes are abnormal are very much dwarfed, being in some instances less than two feet tall. Plants having a smaller number of abnormal internodes approach the normal plants in height and appearance.

Maize, like other monocotyledonous plants, has a region of meristematic cells at the base of each internode. The abnormal internodes are such as would be produced by a more rapid growth in the meristem on the side of the internode of the leaf attachment.

TERMINOLOGY

$Z_1 z_1$,—a factor pair for zigzag culms in maize. This factor pair is linked with the pair $G_1 g_1$.

$Z z$,—a second factor pair for zigzag culms.

$G_1 g_1$,—a factor pair for green-striped leaves (LINDSTROM 1918).

INHERITANCE OF ZIGZAG CULMS

Behavior in the F_1 and F_2 generations

Plants with zigzag culms breed true when self-pollinated. When plants with zigzag culms are crossed with plants with normal culms, the F_1 offspring have normal culms.

Eleven F_2 progenies are listed in table 1. These progenies fall into two well defined groups. The one group has normal and zigzag plants in ratios approaching 15 : 1 and the other group has normal and zigzag plants in ratios approaching 3 : 1. The ratios of the first group vary from 13 : 1 to 19 : 1; those of the second group from 2.7 : 1 to 3.1 : 1. The results are in accord with the interpretation that culm form is determined by two independent factors.

TABLE 1

F_2 progenies of the cross normal × zigzag.

PEDIGREE NUMBERS	NORMAL CULMS	ZIGZAG CULMS	RATIO
Dihybrid			
535	343	23	14.9 : 1
918	207	16	13.0 : 1
919	186	13	14.3 : 1
1525	323	19	17.0 : 1
1526	147	10	14.7 : 1
1530	259	19	13.6 : 1
1531	308	18	17.1 : 1
1532	380	20	19.0 : 1
Total	2153	138	16.2 : 1
Monohybrid			
1527	291	93	3.1 : 1
1528	290	107	2.7 : 1
1529	178	62	2.9 : 1
Total	759	262	2.9 : 1

In crossing zigzag plants with normal plants from various sources it might be expected that some of the crosses would involve both factors for zigzag culms, and others only one. When both factors are involved a 15 : 1 F_2 ratio is expected, and when only one factor is involved a 3 : 1 F_2 ratio. The observed results closely approximate the expectation in both cases. A comparison of the observed distribution with expectation follows:

Group 1	*Normal*	*Zigzag*	*Total*
Observed	2153	138	2291
Expected (15 : 1)	*2148*	*143*	*2291*
Deviation, 5.0 ± 24.7			
Group 2	***Normal***	***Zigzag***	***Total***
Observed	759	262	1021
Expected (3 : 1)	*766*	*255*	*1021*
Deviation, 7.0 ± 9.3			

For each group the deviation from expectation is less than the probable error. Deviations as large as these are to be expected from chance alone in more than one out of every two similar trials.

F_1 plants back-crossed with zigzag plants

Two F_1 plants from the cross, normal × zigzag, were back-crossed with zigzag plants. The same F_1 plants were self-pollinated and gave 15 : 1 ratios in the F_2 generation, thereby indicating that both factors for zigzag culms were involved. The progenies obtained from the back-crosses consisted of normal and zigzag plants in ratios approaching the 3 : 1 relation expected. The numbers observed are given in table 2.

TABLE 2

F_1 progenies of the cross $Z_g z_g Z z \times z_g z_g z z$.

PEDIGREE NUMBERS	NORMAL CULMS	ZIGZAG CULMS	RATIO
255	251	75	3.35 : 1
256	163	56	2.91 : 1
Total	414	131	3.16 : 1
Expected	*408.75*	*136.25*	*3.00 : 1*

Deviation, 5.25 ± 6.8

Further tests of the back-crossed plants

To further substantiate the conclusions drawn, many normal plants from two dihybrid back-cross cultures were self-pollinated or again back-crossed with zigzag plants. The results are given in table 3.

In many of the progenies the number of plants is small and in some the deviation from the expected ratio is quite large. But the dihybrid and monohybrid progenies are sharply separated. The totals for both families are given in table 4.

The expected proportions of genotypes in a dihybrid back-cross population are as follows:

1 $Z_g z_g Z z$, normal dihybrid
1 $Z_g z_g z z$, normal monohybrid
1 $z_g z_g Z z$, normal monohybrid
1 $z_g z_g z z$, zigzag

One-third of the normal plants should give dihybrid progenies when self-pollinated or crossed with zigzag and two-thirds should give monohybrid progenies. Thirty-four normal plants of family 255 were tested and it was found that 12 were dihybrid and 22 monohybrid. Also 28 normal

TABLE 3

Progenies of the back-cross normal plants when self-pollinated or again crossed with zigzag.

PLANT NUMBER	SELF-POLLINATED			CROSSED WITH ZIGZAG PLANTS		
	Normal	Zigzag	Ratio	Normal	Zigzag	Ratio
Family 255						
Dihybrid						
5	61	2	30.5 : 1	15	4	3.75 : 1
6	62	6	10.3 : 1	59	24	2.71 : 1
8	65	5	13.0 : 1			
10				72	23	3.13 : 1
18	83	6	14.0 : 1	58	18	3.22 : 1
27	83	6	14.0 : 1			
29				57	16	3.56 : 1
31	65	5	13.0 : 1	70	24	2.92 : 1
38	71	3	23.6 : 1			
45	69	4	17.2 : 1			
48				58	16	3.62 : 1
64	80	5	16.0 : 1	51	23	2.22 : 1
Total	639	42	15.2 : 1	440	148	2.97 : 1
Expected	*638.5*	*42.5*	*15.0 : 1*	*441*	*147*	*3.00 : 1*
Monohybrid						
7				37	37	1.00 : 1
11				23	24	0.96 : 1
12	56	15	3.73 : 1			
13	58	19	3.05 : 1			
16	67	28	2.40 : 1	19	21	0.90 : 1
20	32	12	2.67 : 1			
21	50	23	2.17 : 1			
22	56	16	3.50 : 1			
24	64	18	3.56 : 1			
25	62	20	3.10 : 1			
28	62	21	2.95 : 1			
30	48	20	2.40 : 1			
32	48	15	3.20 : 1	38	35	1.09 : 1
35	54	21	2.57 : 1			
39	61	20	3.05 : 1			
44	49	25	1.96 : 1			
47	65	22	2.95 : 1			
49	49	15	3.27 : 1			
51	68	25	2.75 : 1			
54	57	20	2.85 : 1			
57	50	16	3.12 : 1	13	4	3.25 : 1
61	56	17	3.30 : 1			
Total	1112	388	2.87 : 1	130	121	1.07 : 1
Expected	*1125*	*375*	*3.00 : 1*	*125.5*	*125.5*	*1.00 : 1*

TABLE 3 (continued)

PLANT NUMBER	SELF-POLLINATED			CROSSED WITH ZIGZAG PLANTS		
	Normal	Zigzag	Ratio	Normal	Zigzag	Ratio
Family 256						
Dihybrid						
23	106	6	17.7 : 1			
26				54	12	4.50 : 1
46	84	8	10.5 : 1			
48				26	9	2.89 : 1
52	47	1	47.0 : 1	27	2	13.50 : 1
56	61	1	61.0 : 1			
57	96	6	16.0 : 1			
58				71	10	7.10 : 1
60				40	15	2.67 : 1
64	92	2	46.0 : 1			
66	57	6	9.5 : 1	52	20	2.60 : 1
67	46	3	15.3 : 1			
Total	589	33	17.85 : 1	270	68	4.00 : 1
Expected	*583*	*39*	*15.00 : 1*	*253.5*	*84.5*	*3.00 : 1*
Monohybrids						
1	137	26	5.27 : 1			
2	53	16	3.31 : 1			
4	43	15	2.87 : 1	4	1	4.00 : 1
5	65	20	3.25 : 1			
6	77	20	3.85 : 1			
8	51	17	3.00 : 1			
18	39	17	2.30 : 1			
24				44	28	1.57 : 1
27	38	34	1.12 : 1			
32	49	14	3.50 : 1			
39				22	25	0.88 : 1
40				39	26	1.50 : 1
43	28	13	2.15 : 1	41	25	1.64 : 1
50	49	29	1.70 : 1	33	19	1.74 : 1
53	56	17	3.30 : 1			
59				11	5	2.20 : 1
Total	685	238	2.88 : 1	194	129	1.50 : 1
Expected	*692.25*	*230.75*	*3.00 : 1*	*161.5*	*161.5*	*1.00 : 1*

TABLE 4

	SELF-POLLINATED				CROSSED WITH ZIGZAG			
	Normal	Zigzag	Total	Ratio	Normal	Zigzag	Total	Ratio
Dihybrid progenies								
Observed	1228	75	1303	16.4 : 1	710	216	926	3.28 : 1
Expected	*1221.5*	*81.5*	*1303*	*15 : 1*	*694.5*	*231.5*	*926*	*3.00 : 1*
Deviation	6.5 ± 18.6				15.5 ± 8.9			
Monohybrid progenies								
Observed	1797	626	2424	2.87 : 1	324	250	574	1.3 : 1
Expected	*1817*	*606*	*2423*	*3 : 1*	*287*	*287*	*574*	*1.0 : 1*
Deviation	20.0 ± 14.4				37.0 ± 8.1			

plants of family 256 were tested and it was found that 12 of them were dihybrid and 16 monohybrid. The totals taken from table 3 are as follows:

	Dihybrid	*Monohybrid*	*Ratio*
Observed	24	38	1 : 1.58
Expected	*20.7*	*41.4*	*1 : 2.00*

Deviation, 3.3 ± 2.5

A deviation as large as this could be expected about once in every three trials, due to chance.

LINKAGE BETWEEN THE FACTOR PAIRS Z_g z_g AND G_s g_s

Plants with zigzag culms were crossed with green-striped plants (LINDSTROM 1918). The F_1 plants were normal both for culm form and for leaf color. Two F_2 distributions involving one of the zigzag factors and the factor for green striping are given in table 5. No green-striped zigzag plants were obtained. The other classes were as follows: 378 plants with green leaves and normal culms (G_s Z_g), 200 plants with green leaves and zigzag culms (G_s z_g), and 203 plants with green-striped leaves and normal culms (g_s Z_g). The absence of green-striped zigzag plants, together with the close approximation to a 2 : 1 : 1 : 0 ratio, indicates close or complete linkage between the factor pair $G_s g_s$ and one of the factor pairs for zigzag culms. To this zigzag factor pair the symbols $Z_g z_g$ have been assigned.

TABLE 5

F_2 progenies of the cross $z_g z_g z z G_s G_s \times Z_g Z_g z z g_s g_s$.

PEDIGREE NUMBERS	GREEN PLANTS		GREEN STRIPED PLANTS	
	Normal	Zigzag	Normal	Zigzag
1527	193	93	98	0
1528	185	107	105	0
Total	378	200	203	0
Expected (complete linkage between z_g and g_s)	*390.5*	*195.25*	*195.25*	*0*
Deviations	−12.5	4.75	7.75	0

χ^2=0.824 P=slightly less than 1.

Table 5 gives a summary of data on F_2 distributions involving green-striped leaves and both factors for zigzag culms. The results are in agreement with the expected ratio (11 : 1 : 4 : 0) for complete linkage between the factor pairs $Z_g z_g$ and $G_s g_s$.

TABLE 6

F_2 progeny of the cross $z_g z_g z z G_s G_s \times Z_g Z_g Z Z g_s g_s$. Family 1525.

	GREEN PLANTS		GREEN STRIPED PLANTS	
	Normal	Zigzag	Normal	Zigzag
Observed	241	19	82	0
Expected (11:1:4:0)	*235.1*	*21.4*	*85.5*	*0*
Deviations	5.9	−2.4	−3.5	0

χ^2=0.561 P=slightly less than 1.

The value of χ^2 for the data in table 5 is 0.824, and for the data in table 6 χ^2 is 0.561. Thus it is seen that in each case the observed numbers are in close agreement with expectation.

SUMMARY

Maize plants with zigzag culms were first observed in a number of F_4 progenies of a cross between Tom Thumb pop corn and a variety of Missouri dent corn. The culms are more or less crooked instead of straight as in normal plants. The affected internodes arch away from the point of leaf attachment, and in many instances the internodes are entirely removed from the leaf sheaths which normally clasp them.

Crosses between normal plants and zigzag plants give F_1 plants with normal culms. Some F_2 progenies consist of normal plants and zigzag plants

in the ratio 15 : 1; others have these phenotypes in the ratio 3 : 1. The data are explained by assuming two independent factors. These factors have been designated Z_g z_g and Z z. Zigzag culms appear only when both factor pairs are recessive.

The factor pair Z_g z_g is very closely or completely linked with the factor pair G_s g_s.

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A RARE CARBOHYDRATE IN WAXY MAIZE

PAUL WEATHERWAX
Indiana University, Bloomington, Indiana

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The dextrins, which occur as successive steps in the transition from glucose to starch and from starch to glucose, are so rarely detected in plant tissues and so ephemeral in existence, that their occurrence in stable form in matured or dormant tissues has seldom been reported. It has been the occasion of no little interest, therefore, to find that the sole carbohydrate in the endosperm of "waxy" maize is the rare erythrodextrin.[1]

This variety of corn has been known to science since 1909, when COLLINS (1909) described it as a new type found in China. Besides possessing certain vegetative peculiarities, it has an endosperm distinctly different from that of other varieties, justifying its recognition as a cultural variety coördinate with the flints, dents, pops, etc.

The grains of waxy corn are rounded and plump, showing no roughened exterior due to shrinkage at maturity. The endosperm, although hard like that of flint corn, is opaque, and shows a dull, smooth fracture.

Since its discovery in China, this variety has also been found in Burma (COLLINS 1920), and its occurrence in these two places has been considered in connection with claims of a pre-Columbian occurrence of maize in the Orient. The peculiar type of endosperm has also been extensively studied genetically. No one, however, seems to have explained, thus far, the chemical and physical basis of the waxy character itself. COLLINS (1909, p. 15) states: "The appearance and physical composition of the seeds of this Chinese corn were so distinct from that of other varieties that the possibility of a difference in chemical composition naturally suggested itself, but analyses did not yield any very unusual results." Then follow data from analyses made by the Bureau of Chem-

[1] A dextrin which is turned red by iodine. Amylodextrin turns blue, and achroödextrin gives no color reaction with iodine. The term "amylodextrin" is sometimes used for all dextrins regardless of their color reactions with iodine. Here and elsewhere in this paper, the iodine reagent to which reference is made is an aqueous solution, of various strengths, of one part of iodine and four parts of potassium iodide.

istry, of twenty-one varieties of corn, including the new Chinese type and a hybrid between it and a corneous variety. Inasmuch as appreciable oil contents are noted, it seems that the whole grains were analyzed, and such an analysis could not be expected to indicate in any accurate way the composition of the endosperm, the structure under investigation.

The nature and quantity of carbohydrate present appear to have been ignored in these analyses. In his extended report on the inheritance of the waxy endosperm, KEMPTON (1919) makes no mention of any further attempts to determine the basis of the peculiarity.

The peculiar texture of the endosperm of waxy maize seems to be determined wholly by the physical properties of the grains of carbohydrate in its cells. The iodine test for starch in this endosperm brings out a rich violet-red color such as is given by no carbohydrate other than erythrodextrin. On microscopic examination the dextrin is found to be in the form of definite grains similar in size and shape to the starch grains of other varieties of maize, but less transparent. This dextrin is soluble in hot water, the solution or viscous suspension giving the characteristic red reaction with iodine. It dissolves very slowly in cold water, probably because of its granular form. It is readily hydrolyzed by diastase.

The only comprehensive account that has been found of this polysaccharide is that by ARTHUR MEYER (1886). From the data accumulated from his own researches and the works of NÄGELI, GRIS, SACHS, TREUB, RÜSSOW, and DAFERT, he finds that starch grains which are turned red by iodine are known to occur in *Iris germanica*, *Chelidonium majus*, *Acer Pseudoplatanus*, *Monotropa Hypopytis*, *Gentiana lutea*, *Swertia perennis*, eight species of orchids, and three cereals. The latter, *Oryza sativa glutinosa*, *Panicum miliaceum glutinosum*, and *Sorghum vulgare glutinosum*, are of special interest here because of their relationship to maize. PARNELL (1921) states that a dextrin of this kind is found in mace and a small group of varieties of rice. This must also be the carbohydrate mentioned by YAMAGUCHI (1918) n a variety of rice which shows xenia when pollenized by other varieties.

In the cases mentioned by MEYER (1886), the dextrin is found sometimes in the seeds and sometimes in vegetative parts of the plants mentioned, its grains often being associated with those of ordinary starch. In the glutinous variety of sorghum it occurs only in the endosperm, the starch of the embryo and other vegetative parts showing the blue reaction with iodine. PARNELL (1921) reports a distinct difference in reaction between the pollen grains of glutinous and starchy varieties of rice.

In waxy maize the erythrodextrin has been found only in the endosperm. The carbohydrate in the embryo is ordinary starch. That in other parts of the plant has not been examined.

The occurrence of erythrodextrin in maize has a significance other than that of a mere addition to a meagre list of plants showing the characteristic. The difference in genetic behavior between waxy corn and sweet corn has a close parallel in the microchemical differences between the two; and the peculiar chemical condition here described for the one may throw into greater relief some of the significant facts about the endosperm of the other.

Geneticists of the past quarter of a century have found in hybrids between sweet and starchy varieties of maize, material readily utilizable for illustrating Mendelian ratios. But in the majority of the experiments reported, the 3 to 1 ratio expected in the conventional F_2 generation (of endosperms) has been complicated by the occurrence of grains intermediate between sweet and starchy. The usual recourse has been the citation of the possibility of a reclassification, based upon the degree of expression of the characters concerned, or an interpretation based upon various observed or assumed conditions. On the other hand, the waxy character of the endosperm behaves as a simple recessive to the corneous condition, the two characters being definitely alternative, "no blending or intermediate stages having been found" (KEMPTON 1919).

The endosperm of sweet corn seems to contain many hexose compounds. The most prominent objects encountered in a microchemical examination are starch grains with rough, eroded surfaces, suggesting partial hydrolysis during maturity of the endosperm. These grade off through a series of smaller grains to an amorphous mass, which becomes glutinous when soaked in water. These carbohydrates are probably starch and amylodextrin, since they give the blue reaction with iodine. The sweet taste, more or less of which remains in the mature endosperm, suggests the presence of achroödextrin, reducing sugars, or sucrose. Mature seeds, however, usually give negative results when tested for reducing sugars. An occasional violet reaction with iodine indicates the presence of some erythrodextrin, but definite grains having this reaction have not been found.

Since the enzymes concerned in the synthesis of the reserve materials in such tissues as this are known to be often reversible with temperature changes, it seems probable that the peculiar organization of the carbohydrates in sweet corn may be due to repeated reversals of the process during the maturity of the seed. This is further indicated by the fluctu-

ating sweetness of sweet corn in the edible stage, depending upon the time of harvesting and conditions of storage.

In contrast with this condition, the endosperm of waxy corn contains but the one kind of carbohydrate, and its grains show no indication of partial hydrolysis as do those of sweet corn.

Sufficient consideration of the fundamental physical and chemical nature of the endosperm of sweet corn in connection with experimental work in the past few years would have done much to clear up a muddled situation by affording a more definite basis for the classification of intermediate grains and of others which have given unexpected genetic results. Much fruitless supplementary experimental work undertaken in attempts to explain unexpected results could have been avoided if the investigator had known definitely with what characters he was dealing, and a better knowledge of the real nature of the characters concerned will doubtless show that such widely divergent views as those of HARPER (1920) on the one hand and the main body of geneticists on the other, are really not so far apart. This clearer understanding would have enabled COLLINS and KEMPTON (1914) to determine the real nature of the grains that resembled starchy corn in contour and sweet corn in heredity, and would have pointed the way toward more conclusive results in JONES'S (1919) work on "pseudo-starchy" endosperm.

The smooth contour of an apparently starchy grain of corn may cover a multitude of possibilities, and the visual method of discriminating between endosperm textures by observing the outside of the grain is as crude as a color-blind man's attempt to describe the rainbow. That intermediates between the two widely different types of endosperm (sweet and starchy) do occur is not to be doubted, and many grains apparently sweet or starchy will doubtless fall into intermediate classes as our vision becomes keener. From what we know at present, nothing less than the assumption of many factorial differences between sweet corn and starchy corn will be in accord with our genetic and histological data, and even then a generous allowance must be made for the effect of environment.

Of geographical interest, although without any significance known at present, is the generalization that all four of these cereals,—rice, sorghum, millet, and maize,—known to have erythrodextrin in their endosperms, have been first found in eastern Asia and the adjoining islands.

Waxy maize has doubtless arisen from starchy maize by mutation, and the nature of its endosperm indicates that its origin has been as simple as that of sweet corn, since only the size of the molecule of reserve material has been affected. Inasmuch as the sporadic appearance of

sweet corn as a mutant from starchy corn in many parts of America, is known, the occurrence of waxy maize in China and in upper Burma is probably of no great significance as an indication of the pre-Columbian occurrence of maize in Asia.

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HEREDITY OF ANGIONEUROTIC EDEMA BASED ON A REVIEW OF THE LITERATURE

JAMES McILVAINE PHILLIPS
Pasteur Institute, Columbus, Ohio
AND
WILLIAM MORTON BARROWS
Ohio State University, Columbus, Ohio

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Angioneurotic edema is manifested clinically by sudden swellings of the skin or mucous membranes, which persist for a few hours to several days, and disappear as quickly as they come. There may be only a single outbreak during the life of an individual or the swellings may occur at irregular intervals with greater or less frequency, so that in some cases the life of the victim may become burdensome. In some cases the attacks are periodic. The size of the swellings varies, at times being enormous. In certain positions they may cause death by mechanical interference with one of the vital functions. This is most common in edema of the glottis.

The disease may appear in childhood or it may not be noticed until past middle age. Usually it becomes less annoying as old age approaches.

In the past the causes of the disease were given by various authors as "nervous influences," "infections," "disorders of the endocrine glands," and "dietetic errors." At present allergy would seem to be the most plausible explanation and this is substantiated in certain types of the disease. Whether allergic individuals are born hypersensitive to specific substances, or whether they are born with a tendency to become easily sensitized is still a much disputed subject. COCA (1920) is quite positive that, unlike experimental anaphylaxis, it is not an antibody-antigen reaction. On the other hand, SCHLOSS (1920) reports the passive transference of sensitization from children to guinea-pigs by means of the blood serum.

However this may be, it is known that in some cases the ingestion of certain foods causes the attack and that when these foods are not eaten, the attacks do not occur, and that in many of these, but not all, a positive skin test to the protein of the offending food can be demon-

strated. In some cases where the skin tests are positive to specific foods, abstinence from them does not always prevent the attacks. In others the disease may be shown clinically to depend on a food and the skin test to it may be negative even though its removal from the dietary apparently prevents the outbreaks.

From a clinical standpoint these definitely allergic cases may be roughly grouped into two types which we will designate as the prompt and the delayed.

In the prompt type within a comparatively short time after the offending protein is taken, nausea, vomiting, and perhaps diarrhoea, appear, and these are quickly followed by areas of pruritis and wheals which rapidly coalesce. The edema soon assumes remarkable proportions especially about the head and neck. Skin tests are often positive. Adrenalin may be potent to control the attack. In many individuals some of the outbreaks never go beyond the urticarial stage, while others become edematous.

This type of angioneurotic edema closely resembles certain cases of general allergic reaction which are produced in hypersensitive individuals when they are injected with the various substances to which they react. (WALKER 1918; COOKE 1922.)

In the delayed type some hours or even days may elapse after the ingestion of the offending food before symptoms appear. The lesions are usually single and commence with a slight tingling or pricking sensation, and expand with remarkable speed until they become superwheals. Gastro-intestinal crises may or may not be present. Adrenalin, even when injected into the swellings, is apparently valueless in controlling them. As a rule, skin tests are negative, but there are exceptions, so that the determination of the offending substance rests upon a clinical basis only. For this reason the cause of the disturbance is not ascertained in many cases which are definitely hypersensitive; consequently, their treatment is unsatisfactory and difficult.

OSLER (1897) suggests that changes occurring in the food during some stage of its sojourn in the body may be responsible for some of these cases.

Since the time of QUINCKE (1882) angioneurotic edema has been recognized as heritable, and indeed many authors state that it seems to be a Mendelian dominant, but we know of no one who has made an analysis of the reported families. From a genetic standpoint the disease can be classified as sporadic and familial.

SPORADIC ANGIONEUROTIC EDEMA

The so-called sporadic cases deserve minute investigation. Allergy is certainly the fundamental condition in most of them, and the family history often reveals the presence of eczema, urticaria, hay-fever, asthma, etc. An example of this is shown in figure 1 (PHILLIPS 1922). Indeed, its association with these diseases, which also depend upon allergy, is so common as to suggest the possibility that the heredity of these diseases depends upon more than one factor.

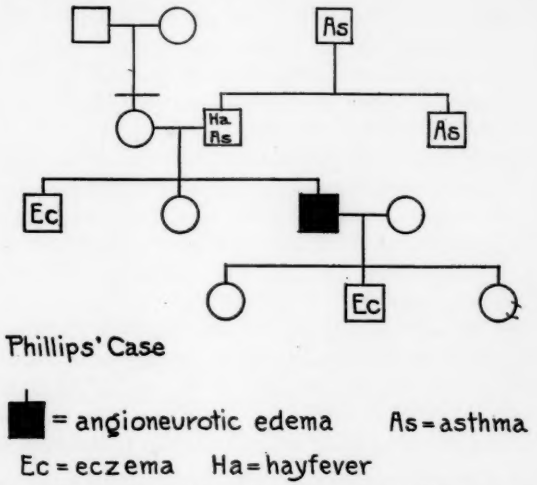

FIGURE 1.—From PHILLIPS (1922), illustrating a sporadic case in which eczema and asthma are familial traits. Note that in this family all males are affected with some manifestation of sensitization.

It may be noted here that the visible lesions of allergy are those of hyperemia and edema. Thus in the skin test (BROWN 1922) a positive result is shown by erythema followed by the formation of a wheal, with irregular outlines and pseudopod-like extensions of the edema, which apparently follow the course of the lymphatics. In the erythemas the hyperemia is more noticeable than the edema. These conditions are reversed in urticaria. Hay-fever is characterized by the development of a similar hyperemia and edema of the mucous membranes of the eye, nose and throat. However, the appearance of this edema is somewhat modified by a secondary bacterial infection of the swollen mucous membrane. Certain types of eczema would seem to show a like series of changes

occurring in the skin. These are further complicated by trauma, inflicted by the patient as he scratches his itching skin, and by secondary infection.

Most authors consider asthma due to a spasm of the non-striated muscle of the bronchi, but the appearance of the mucous-membrane lining of the trachea and bronchi, as described by FREUDENTHAL (1912) who viewed them through the bronchoscope during attacks, would seem to show definitely that here again we have erythema and edema of the mucous membrane.

The rheumatoid pains so often associated with urticaria and angioneurotic edema, are probably due to a similar condition of the serous membrane of the joints.

In angioneurotic edema this edema seems to be more generalized and intense, so that the skin, mucous, and serous membranes, and their underlying connective tissues, are all affected.

As all of these diseases are well known to be heritable, and are often associated as family traits, it would seem that the main difference between them lies in the distribution of hypersensitive tissues and in the intensity of their reaction. The cause of these patterns of distribution of hypersusceptibility of the tissues and the variation in its intensity should be investigated by the geneticist.

The solution is rendered difficult not only because the hypersensitiveness is not specific, as various members of the same family respond to different proteins, but also on account of the varying age at which symptoms appear. COOKE and VANDERVEER (1917) have called attention to the fact that symptoms occur earliest in those individuals who inherit this tendency from both parents. They consider allergy as a dominant trait while ADKINSON (1920) investigating the heredity of asthma as a specific disease, concluded that it was a recessive.

Another of the many difficulties is that a person may be hypersensitive, but, unless the environment is such that he comes in contact with his allergic substance, he will remain ignorant of his condition. Thus we know of one family of Germans in which ragweed hay-fever appeared for the first time in many of its members the very first fall after immigrating to this country, those afflicted ranging in age from the grandfather to a young child. Such persons might easily appear in a pedigree as normals.

Despite all these obstacles we believe that full pedigrees of victims of angioneurotic edema of the sporadic type from hypersensitive families, including all normal members as well as those afflicted with the various clinical types of allergy, might aid much toward unraveling this mystery.

FAMILIAL ANGIONEUROTIC EDEMA

In the familial types the attacks appear generation after generation in many members of the afflicted families and exact a heavy toll of suffocative deaths caused by edema of the glottis. These characteristics are shown in figure 2. The symptoms are so like those occurring in the sporadic type that it is generally considered to be an identical condition, but we are not aware of the skin reactions of any of these families having been made the subject of research by the immunologist. Studies of the protein reactions in one of these families, together with a complete family history covering all diseases of allergic origin, might do much toward solving the problem of the heredity of human allergy.

A careful study by matings of the twenty-seven pedigrees published in the Treasury of Human Inheritance (BULLOCK 1909), which appears to bring the data up to its date, together with the pedigrees of BOLTEN (1919), CAMERON (1920), CROWDER and CROWDER (1917), and EDGERLY and LUSK (1919), which have been published later, has been summarized in tables 1 and 2.

TABLE 1

Affected × unaffected.

CHARACTERISTICS OF PROGENY	MALE PARENT AFFECTED. 56 MATINGS			FEMALE PARENT AFFECTED. 46 MATINGS			SUMMARY 102 MATINGS			
	Offspring	Percent		Offspring	Percent		Sum	Sex?	Sum	Percent
Affected males	70	35	53.1	29	27.6	44.9*	99	3	168	50.15
Affected females	45	22.5		21	20		66			
Unaffected males	47	23.5	47.1*	27	25.7	55.1*	74	27	167	49.85
	— 17†			— 10†						
Unaffected females	38	19		28	26.7		66			

*Including those of unknown sex.
†Sex unknown.

From tables 1 and 2 it will be seen that only two types of matings occur in the pedigrees, namely, matings of affected individuals with unaffected and matings of unaffected with unaffected. Taking up the matings of affected × unaffected first (table 1), the figures show conclusively that familial angioneurotic edema may be transmitted by either parent equally well, the disease appearing in approximately half of the offspring. When the male parent is the one affected the proportions of

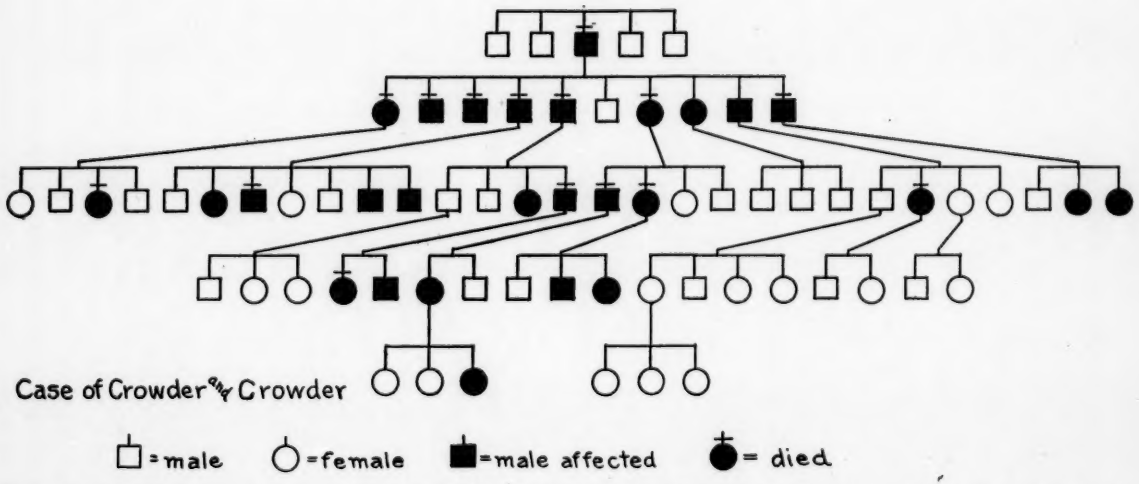

FIGURE 2.—From CROWDER and CROWDER (1917), illustrating a typical familial angioneurotic edema. Note the high mortality due to glottis edema.

TABLE 2

Neither parent affected.

CHARACTERISTICS OF PROGENY	PRODUCING NO AFFECTED PROGENY	PRODUCING AFFECTED PROGENY	
	One grandparent* affected 27 matings	One grandparent affected 10 matings	Grandparents unknown 6 matings
Affected males	0	12	6
Affected females	0	5	3
Unaffected males	32	6	2
Unaffected females	49	7	3

*In one mating the great-grandparent only was affected.

affected are larger than would be expected. This difference is in the opposite direction when the female is the affected parent. Affected males are more numerous than affected females. This is what one would expect since males are more numerous in the whole population. However, the excess of affected males over unaffected males (99–74 = 25) is considerable when compared with the females among which the affected and unaffected are equal in numbers. Many authors still consider human sensitization as an expression of anaphylaxis. If familial angioneurotic edema proves

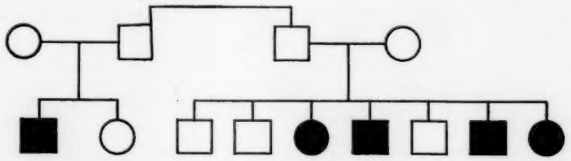

FIGURE 3.—From EDGERLY and LUSK (1919), illustrating two unaffected brothers mated to unaffected females, each producing affected offspring.

to be due to allergy, this type of inheritance forms a striking contrast to the so-called inheritance of laboratory anaphylaxis in which the offspring of the females only are affected because the sensitization is due to a passive transfer of antibodies. If table 1 were our sole source of material we would say without hesitation that angioneurotic edema is a dominant trait and that all matings recorded in the table were of the DR × RR type, giving DR and RR offspring in equal numbers. The

matings recorded in table 2 throw considerable doubt on this interpretation.

For the sake of ease in analysis table 2 is divided into two parts according to the progeny. The second of these groups is again divided on the basis of whether the grandparents were affected or were unknown. The second category probably belongs with the first, but since nothing is known about the grandparents it is of little value. The results recorded in the first column of the table show that we are here dealing with parents which are recessives, i. e., normals, the matings being of the type RR × RR giving RR offspring only. This is what would be expected if the trait were a dominant. Each of the ten matings recorded in the next column produced affected individuals. These with the six matings of the next column indicate that in sixteen out of a total of forty-three matings, or 37 percent, the parents carried the trait without showing it. These figures are too large to be due entirely to accidental errors.

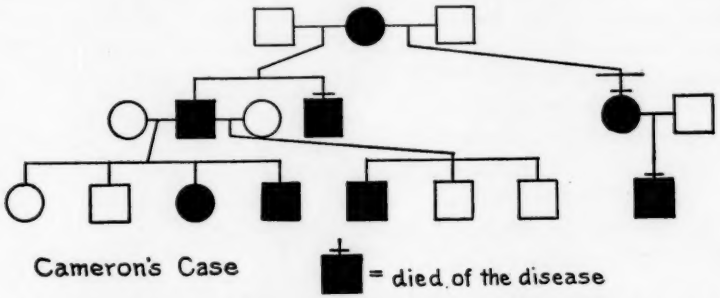

FIGURE 4.—From CAMERON (1920), illustrating the typical dominant type of inheritance through two double matings.

Two other explanations are possible; firstly, that angioneurotic edema is due to a fundamental condition which requires some specific stimulus to disclose it and that these cases were potentially affected but were not exposed to the proper stimulus to make the disease appear; or secondly, that the condition is due to two factors which are closely linked. If the second explanation is the correct one, each of two unaffected parents supply one of these factors, which after crossing over are transmitted together more often than they are separated. This would account for their inheritance in most cases as a dominant trait. It would also account for the occasional production of an affected individual from two unaffected parents each alone incapable of producing edema. One of these fac-

tors may very likely be the factor which makes the bearer respond to some exciting substance by developing asthma, eczema, hay-fever, or urticaria. The other factor, if such is present, is either similar to the first or unknown. That urticaria, asthma, eczema, hay-fever and other allergic conditions

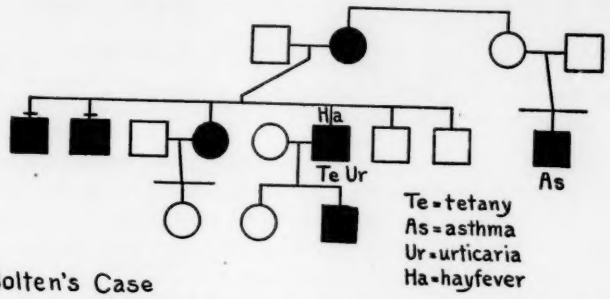

FIGURE 5.—From BOLTEN (1919), illustrating familial angioneurotic edema associated with other manifestations of allergy.

are very common in families where angioneurotic edema occurs has long been known. Sometimes angioneurotic edema and asthma are found together in the same person as in BOLTEN'S (1919) case, figure 5. In this case the patient had angioneurotic edema, urticaria, perennial hay-fever and tetany, while a cousin had angioneurotic edema and asthma.

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HOLOGYNIC HEREDITY

PAOLO ENRIQUES
Istituto di Zoölogia e Anatomia Comparata, Padova, Italy

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Sex-linked characters in man are well known; they are all pathological characters, so far as known; they are transmitted according to the same laws as the sex-linked characters in the little fruit-fly (Drosophila) and explained in the same manner by means of the sex chromosome.

I propose the name "diagynic heredity" for this kind of heredity, as the sex-linked character is transmitted from male to male, not directly, but through the unaffected females (e. g., hemophilia, daltonism).

In the currant moth (*Abraxas grossulariata*) the character "*lacticolor*" is transmitted from female to female, not directly, but through the "unaffected" males. This "dia-andric heredity" is not known in man.

A third kind of sex-linked heredity is possible. We know two pedigrees of this kind (daltonism, hemophilia), and two new pedigrees are referred to in this paper (hemophilia, cataract). No one has considered this special kind of heredity or noticed its theoretical and practical importance.

For the pedigree of daltonism (CUNIER), see PLATE 1913, p. 379. Daltonism is usually diagynic; but in this pedigree 12 females are affected in 5 generations. The authors have not emphasized the circumstance that *all* the females are affected. The males are all unaffected. The transmission is direct from the affected female to her daughters.

In another pedigree of hemophilia (GRANDIDIER, see PLATE 1913, p. 379), an affected mother has three affected daughters and no other children; her parents, according to the reference, are unaffected.

I propose for this type of heredity the name of "hologynic heredity."

"Holo-andric heredity" has not been recognized, heretofore, but in the *Journal of Heredity* for November 1921 RICHARD SCHOFIELD has published a pedigree of webbed toes with 14 affected males in 4 generations (all the males) and not one female. SCHOFIELD does not recognize in this pedigree a new form of heredity and thinks that this hereditary trait is inherited as a secondary sex character. But why are *all* the males affected?

This is probably the first known case of holandric heredity.

Two other pedigrees of hologynic heredity will be presented here. The first is very small and concerns again hemophilia (figure 1). In the third generation the first daughter is probably becoming affected, but this is not yet certain.

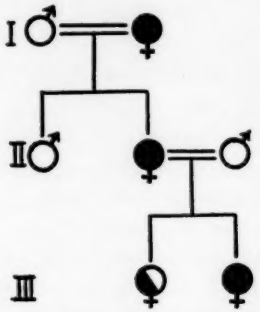

FIGURE 1.—Pedigree chart of a family showing hemophilia in the female line,—hologynic hemophilia.

Much more interesting is the second pedigree, of senile cataract (figure 2). My friend, Prof. GILBERTO ROSSI, the well known physiologist in Florence, has had the kindness to compile this pedigree and permit me to publish it. I am much indebted to him for this.

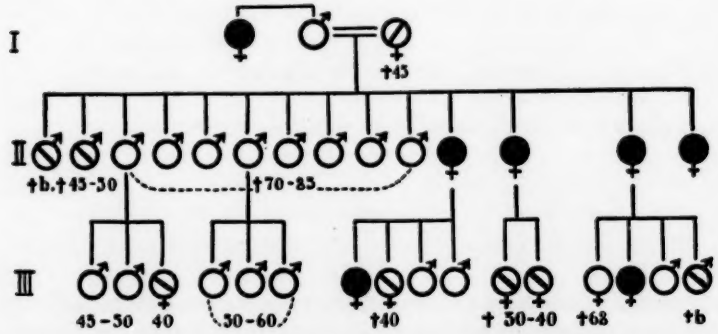

FIGURE 2.—Hologynic senile cataract. The numbers indicate the age that the individual, if living, now has, or the age at death. An oblique line from left to right indicates that the individual has not reached the age in which the cataract developed; from right to left that no information is available as to whether the individual was affected or not; b indicates that the individual died as a child.

In the family of this pedigree, as the females approach the age of 50 years they expect to become affected with cataract. Really only one female has had the good luck to constitute an exception to this rule; she has reached 68 years with good sight. Fourteen males have arrived at or surpassed 50 years, but not one of them has become affected.

The pedigree begins with a couple of which little information about the female is available, except that she died at an age (45) at which the affection is not noted at all in the other females of this family. The sister of her husband was affected.

We cannot determine from this pedigree, or from the others of hologynic heredity, whether the males can be conductors; it is not known whether the cataract is brought into the family by the male of the first generation as a conductor, or by the female.

Notwithstanding the fact that this pedigree is not so extensive as to solve all the questions which suggest themselves, it is clear that we have before us here a new form of heredity.

The direct transmission from female to female and the affection of *all* the females exclude it as a case of dia-andric heredity; the number of the affected females and of the unaffected males exclude also the hypothesis that the affection might be dominant and independent of sex.

The same conclusion is justified in the case of hemophilia. This affection is usually diagynic and females are usually unaffected, for affected females could be born only if the father is affected and the mother is a conductress. But DAVENPORT (1911) has published a pedigree of hemophilia with some affected females. He noted this abnormality, but did not point out that the method of transmission is in this case very different from the usual diagynic; the hemophilia is here dominant and independent of sex. There are two other unusual pedigrees of hemophilia, one of GRANDIDIER, and the one referred to in this paper (figure 1), in which only the females are affected.

Daltonism is usually inherited as a diagynic trait; but an unusual pedigree is known with affected females, and in this case all the females (12) are affected, with direct transmission, and not one male. It is not admissible to assume that in all these cases the affection is a dominant one, independent of sex, and that by chance only females (all the females) are affected. Such a possibility exists, to be sure; if we find a short pedigree of this kind among ten thousand ordinary pedigrees of brachydactyly, for instance, this may be by chance. But we know only three extraordinary pedigrees of hemophilia, with many affected females, and in two of these all the females are affected; of two cases of daltonism one is also of

this kind. The pedigree of cataract shown in figure 2, also can not be reasonably explained on the ground of chance.

Thus, a new kind of heredity exists, sex-linked, but not diagynic or dia-andric,—hologynic heredity. The features of this heredity are not yet known, but its existence seems to me to be certain. Provisionally I suppose that these features are very simple: (1) The daughters of an affected mother are all affected; (2) The sons of an affected mother are all unaffected and not conductors.

How can hologynic heredity be explained? The coexistence of diagynic and hologynic heredity in the same species makes the explanation very difficult. Nevertheless, I will make an attempt in this direction.

The diagynic heredity requires the existence of two kinds of spermatozoa, one of which possesses the X chromosome, the other not. Naturally, it is possible that paired with the X chromosome there is a Y chromosome, different from X, and destined to remain always in the male line. That is really the case in some kinds of insects. If one should discover a holandric heredity in the insects, its explanation would be very easy; the Y chromosome, which remains in the male line, could well explain a sex-linked character which remains always in the male line.

But we have to explain a hologynic, not a holandric, heredity. We can imagine a scheme like that for the dia-andric heredity, with two kinds of eggs and a W chromosome which remains always in the female line. W can transmit the cataract or the hemophilia or the daltonism.

This explanation or a similar one is logically suggested by the observed facts. It is necessary to suppose that something remains in the female line and can not be transmitted by the male. Then an egg possesses this thing or does not possess it, according to its sex. This would require that the sex be determined already in the egg, independently from the spermatozoön and fertilization.

I consider this almost a logical consequence of the facts. It is possible, however, that, for example, the hologynic hemophilia is transmitted by something that is in all the eggs of an affected female, independent of sex, and that the male-determining spermatozoön destroys this thing. But this mechanism is entirely different from the chromosomal mechanism which explains the heredity of the diagynic hemophilia or of the not-sex-linked dominant hemophilia. It seems too improbable that the same character can be transmitted by two entirely different mechanisms; we can suppose that in one family one chromosome transmits it, in another family another chromosome, but the mechanism of the transmission must

be the same in all cases. Therefore, there should be two kinds of eggs, and two kinds of spermatozoa, in order to explain the diagynic heredity.

This hypothesis requires a selective fertilization; the male-determining egg must be fertilized by a male-determining spermatozoön and the female-determining egg by a female-determining spermatozoön.

The following scheme will explain this type of heredity: Let F be the chromosome which always remains in the female line; so that a pair, Ff, in the female corresponds to a pair, ff, in the male; and let M be the Y chromosome and m the X chromosome. Then a mating will result in the following combinations, the impossible combinations being written in parenthesis:

P_1	Mmff	mmFf
Germ cells	Mf or mf	mF or mf
F_1	Mmff or (MmFf)	mmFf or (mmff)

The hologynic character is transmitted by F. This scheme allows also for the possibility of a holandric character transmitted by M.

The diagynic character is transmitted by m; the scheme provides also for a dia-andric transmission which can be made by f.

This scheme can also be stated in a simpler form as follows:

P_1	m—	mmF
Germ cells	m or —	mF or m
F_1	m or (mF—)	mmF— or (mm—)

This is the simplest symbolic expression of sex-linked heredity in man (diagynic and hologynic). But M is also necessary to explain the holandric heredity, and this is permitted by the type of sex chromosomes which was described in man by WIEMAN (1917).

If we consider sex-linked heredity in a general way, we are surprised by the circumstance that in some insects the female is heterozygous (e. g., in the Lepidoptera), while in all the others the male is heterozygous. It seems that the heterozygous constitution of the male is the more general condition in animals. Heterozygous females are observed only in the Lepidoptera and in birds. This difference, even in the same class, is very difficult to explain; we cannot understand why the chromosome pair XX of the female and the single X chromosome of the male can be replaced by an inverted condition. But if we take the hypothesis of an Mmff group in the male and an mmFf group in the female as a primitive arrangement, we can easily explain the reverse cases. It is possible that in some species certain chromosomes have disappeared before reduction, in which case the possibility of certain kinds of heredity has been lost.

Is the hypothesis of a selective fertilization a very improbable one? Some other facts seem to support the same hypothesis.

In the great fly, *Calliphora erythrocephala*, the sex ratio is exactly 1 : 1 in the best conditions of life. The experiments of Mrs. VALENTI (1913) with many isolated couples of this species have demonstrated that the sons and the daughters of one couple are too often exactly equal in number, or almost equal, than would result from statistical law, and there must be a mechanism by which this result is obtained. We can assume that the mechanism consists in a sexual division, namely, in the production of a male egg and a female egg from a neutral cell; then the eggs of both sexes are equal in number and if they all develop, the sons and the daughters are also equal in number. On the other hand, it is known that in flies the male is heterozygous, and that consequently there is an equal number of male and female spermatozoa; a selective fertilization is the logical corollary of these facts.

I must admit that from seeking an explanation of sex-linked heredity in man, I have been led to the hypothesis of a selective fertilization, a result which has exceeded my original purpose. Although it is a logical consequence, I express it, nevertheless, with some reserve, for I know how dangerous and doubtful is the application of logic to experimental science when data are still inadequate. Future researches may be expected to decide the question.

It is remarkable that a hologynic or diagynic character in man can also be transmitted in a more ordinary way as a dominant one, independent of sex. No sex-linked character is known in man, which behaves as a sex-linked character in all the families in which it appears. Hemophilia is the classical instance of diagynic heredity; now we also know two short pedigrees of hologynic hemophilia, and a pedigree of dominant hemophilia. Many affections of the eye follow the diagynic method of heredity; but some pedigrees are hologynic and others non-sex-linked dominant; e. g., nystagmus, myopia (?), daltonism, hemeralopia, neuritis optica. Cataract has been known only as a dominant character. Now a case of hologynic cataract is discovered.

The explanation of this variability is very simple if the chromosome scheme formulated above is accepted. The character can be transmitted by one chromosome or by another chromosome; there are three possibilities, the chromosome m, F or an autosome. So far as is known, the character is always transmitted, in any given family, by the same chromosome. So we can enunciate three principles which seem to apply to the sex-linked characters in man:

1. Sex-linked characters in man can also be transmitted as ordinary non-sex-linked dominants.

2. Sex-linked heredity in man is diagynic or hologynic; some characters (all?) are transmissible as hologynic and as diagynic. Perhaps a holandric heredity also exists.

3. In a single family, each sex-linked character is transmitted according to a constant method (by the same chromosome). This principle needs further confirmation.

Each sex-linked character of other animals, so far as is known, is transmitted only according to a single rule, always as sex-linked.

Hologynic heredity is known only in man.

The third principle, if confirmed, will constitute a further proof of the individuality of the chromosomes in man.

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AN ATTEMPT TO IMPROVE THROUGH SELECTION THE STYLE LENGTH AND FERTILITY OF *OENOTHERA BREVISTYLIS*[1]

BRADLEY MOORE DAVIS

University of Michigan, Ann Arbor, Michigan

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In an earlier paper (DAVIS 1918) there were published some observations on a selfed line of *Oenothera brevistylis* which had been carried for two generations through plants selected for greater variation in the direction of normal styles and stigmas. The line has now passed through five generations of selection, and not only has there been no improvement but the generations of later years have shown a retrogression so positive as to lend no encouragement to further effort. Apparently the variations in style length and fertility of *Oenothera brevistylis* are not due to heritable factors and consequently there can be no permanent success in selection for the improvement of these characters.

The history of the first two generations has been published in detail (DAVIS 1918, pp. 520–524) and requires but brief review. *Oenothera brevistylis* differs from *Oe. Lamarckiana* chiefly in its short style and reduced stigma which generally lies near the top of the calyx tube instead of at a point above the tips of the anthers. With this poor development of the style and stigma is correlated a very low degree of seed production, the ovaries ripening few or no seeds. There is, however, much variation among different plants of *brevistylis* and between flowers on the same plant with respect to the length of style, and occasionally the stigma will be present at the level of the lower tips of the anthers or somewhat above them. In these flowers the stigma lobes are generally found to be more normal in size and appearance. Although such styles are far from the full length which in *Lamarckiana* is above the anthers, they nevertheless do present a marked variation in that direction and suggest the possibility of selection for permanent improvement of this character. Such longer-styled flowers with more perfect stigmas have a distinctly greater degree

[1] Genetical studies on Oenothera XI. Contribution from the Botanical Laboratory, UNIVERSITY OF MICHIGAN, No. 188.

of fertility and it is possible by persistent selfing, in spite of many failures, to obtain from them a few seeds.

The selection of an individual in each generation to carry on the selfed line was based on a test of performance of all of the plants in each culture. The test, introduced with the second generation, consisted in recording the length of style in the series of flowers opening along the main stem of each plant over a definite period of time. After the first generation the styles were listed as in three grades, *long* when the stigma reached above the lower tips of the anthers, *medium* when the stigma lay between the lower tips of the anthers and the top of the calyx tube, *short* when the stigma was at or below the top of the calyx tube. A full record of the performance of the plants in the first and second generations of the selfed line is given in tables 6 and 8 of the paper cited (DAVIS 1918) and will not be repeated.

The best individual, 16.2d, IV-4, from the first generation of 8 plants, showed a record between July 18 and August 3, 1916 of 19 long-styled and 0 short-styled flowers, a percentage of 100. In this first generation styles were recorded as long when they extended well above the top of the calyx tube and as short if the stigma was at or below the level of the calyx tube. There were selfed 14 flowers of this best individual which set 8 capsules with a total of 104 seeds. The poorest record of this generation was that of a plant which bore 9 long-styled and 7 short-styled flowers over the same period of time and on which 12 selfings gave 7 capsules with a total of 18 seeds.

The second generation consisted of 33 plants from the 104 seeds set by the selected individual, 16.2d, IV-4, of the first generation, the performance of which is given in the paragraph above. There was a wide range of performance in this generation between June 30 and July 28, 1917. The culture presented 6 plants with high percentages of long-styled flowers as follows, 76.9, 75.0, 73.5, 69.2, 65.5 and 64.7, but none of these was chosen as parent for the third generation because they gave either no seed when selfed or the yield was small (DAVIS 1918, table 8). The plant selected to carry forward the selfed line, 17.2, V-1 ripened 54 seeds from 11 capsules after selfing 24 flowers, and produced over the period of observation 19 long-styled, 9 medium-styled and 3 short-styled flowers, a record of 61.3 percent of long-styled flowers. The poorest plant of the second generation bore 0 long-styled, 12 medium-styled and 19 short-styled flowers. The record of the culture as a whole was much below that of the first generation, as indicated in table 7, although the two generations cannot be compared with strict accuracy because of

the different system of recording style length introduced with the second generation.

The parent of the third generation was 17.2, V-1 described in the preceding paragraph. Its seeds, being soaked in water 24 hours, were forced to complete germination in a Petri dish following alternate exhaust and pressure up to 75 pounds applied 4 times in the course of 24 hours. As shown in table 1 the 54 seeds from 11 capsules gave 11 seedlings, a germination percentage of 20.4, and 10 *brevistylis* plants reached maturity.

The 10 plants of the third generation (table 2) made a record somewhat worse than that of the second generation and was far below that of the first. Its best performance, by plant 19.2, I-3, from July 7 to July 25, 1919, was 23 long-styled, 9 medium-styled and 4 short-styled flowers, a record of 63.9 percent long-styled flowers. There were selfed 21 flowers which set only 5 capsules with a total of 15 seeds, a very low degree of fertility. The second-best plant in the culture produced 20 long-styled, 8 medium-styled and 6 short-styled flowers over the same period of time, a percentage of 58.8 long-styled flowers. As shown in table 2 the remaining 8 plants of the culture had percentages of long-styled flowers ranging from 3.3 to 28.6, all very bad records.

TABLE 1

CULTURE	PARENT PLANT *brevistylis*	SEEDS SOWN	NUMBER OF SEEDLINGS	PERCENTAGE OF GERMINATION	PLANTS REACHING MATURITY
19.2	17.2, V-1	54 11 capsules	11	20.4	10

The best plant of the third generation, 19.2, 1–3, was selected as parent of the fourth. Its 15 seeds from 5 capsules after selfing 21 flowers were forced to complete germination in Petri dishes after being soaked in water and following alternate exhaust and pressure up to 45 pounds. Complete germination gave 4 seedlings, of which 2 died early, so that only 2 plants reached maturity; the germination was 26.7 percent (table 3).

The fourth generation, therefore consisted of 2 plants the performance of which between July 12 and August 2, 1920 is given in table 4. The best of these plants, 20.2–1, with 7 long-styled, 16 medium-styled and 15 short-styled flowers made a record of only 18.4 percent long-styled flowers. From 25 selfed flowers 7 capsules were set which ripened 18 seeds. The other plant presented a record of 13.9 percent long-styled flowers.

The 18 seeds from the best plant of the fourth generation, 20.2–1, after 24 hours in water, were subjected to alternate exhaust and pressure up to 30 pounds 10 times in 24 hours. Complete germination yielded 8 seedlings, a percentage of 36.4 (table 5); 6 plants reached maturity.

TABLE 2

Performance in the third generation of brevistylis in a selfed line. Observations from July 7 to 25, 1919.

PLANTS	NUMBER OF FLOWERS OBSERVED	LONG-STYLED	MEDIUM-STYLED	SHORT-STYLED	PERCENTAGE OF LONG-STYLED FLOWERS	YIELD OF SEED FROM SELFED FLOWERS
19.2, I–3	36	23	9	4	63.9	21 flowers selfed gave 5 capsules with 15 seeds
19.2, II–3	34	20	8	6	58.8	
19.2, I–5	35	10	11	14	28.6	
19.2, I–4	32	8	15	9	25.0	
19.2, II–4	30	7	9	14	23.3	
19.2, I–2	32	5	10	17	15.6	
19.2, II–5	35	5	14	16	14.3	
19.2, II–1	24	3	5	16	12.5	
19.2, I–1	33	3	10	20	9.1	
19.2, II–2	30	1	9	20	3.3	

TABLE 3

CULTURE	PARENT PLANT *brevistylis*	SEEDS SOWN	NUMBER OF SEEDLINGS	PERCENTAGE OF GERMINATION	PLANTS REACHING MATURITY
20.2	19.2, I-3	15 5 capsules	4	26.7	2

TABLE 4

Performance in the fourth generation of brevistylis in a selfed line. Observations from July 12 to August 2, 1920.

PLANTS	NUMBER OF FLOWERS OBSERVED	LONG-STYLED	MEDIUM-STYLED	SHORT-STYLED	PERCENTAGE OF LONG-STYLED FLOWERS	YIELD OF SEED FROM SELFED FLOWERS
20.2–1	38	7	16	15	18.4	25 flowers selfed gave 7 capsules with 18 seeds
20.2–2	36	5	11	20	13.9	

The performance of the 6 plants in the fifth generation (table 6), taken between July 20 and August 9, 1921, was somewhat better than that of the fourth, but not so good as that of the third, and it was far below the records of the first and second generations. Its best plant, with 14 long-styled, 13 medium-styled and 10 short-styled flowers, made a record of 37.6 percent long-styled flowers as contrasted with records of 76.9 percent and 63.9 percent for the best plants of the second and third generations, respectively. The other five plants of the culture had records for long-styled flowers ranging from 22.2 to 9.7 percent (table 6), which were very poor performances.

TABLE 5

CULTURE	PARENT *brevistylis* PLANT	SEEDS SOWN	NUMBER OF SEEDLINGS	PERCENTAGE OF GERMINATION	PLANTS REACHING MATURITY
21.2	20.2–1	18 (7 capsules)	8	36.4	6

TABLE 6

Performance in the fifth generation of brevistylis in a selfed line. Observations from July 20 to August 9, 1921.

PLANTS	NUMBER OF FLOWERS OBSERVED	LONG-STYLED	MEDIUM-STYLED	SHORT-STYLED	PERCENTAGE OF LONG-STYLED FLOWERS
21.2–6	37	14	13	10	37.6
21.2–3	36	8	16	12	22.2
21.2–2	33	6	13	14	18.2
21.2–5	35	6	15	14	17.1
21.2–1	39	6	18	15	15.4
21.2–4	31	3	12	16	9.7

Thus instead of improvement in the length of style as the result of selection for these five generations there took place a marked retrogression. The records of the third, fourth and fifth generations were far below those of the first and second. This retrogressive movement is clearly expressed in table 7 which gives the distribution of the plants for all generations grouped in percentages of long-styled flowers. There is no suggestion in this table of probable or permanent advance in style length.

As has been stated, there is correlated with the poor development of the style and stigma of *Oenothera brevistylis* a very low degree of seed production. On this subject it is difficult to obtain much data because so few capsules set any seed that a very large number of pollinations must be

made to obtain harvests worth consideration. In choosing parent plants for the five generations of this selfed line it was of course necessary to pick individuals that produced enough seed to ensure a progeny and in some cases plants with better records of performance in style length could not be used because they ripened either no seed at all or so few seeds that there was no prospect of a satisfactory succeeding generation. This was particularly true of the large second generation (DAVIS 1918, table 8) in which for this reason 6 plants were discarded although their percentage records of long-styled flowers were somewhat higher than that of the plant selected to carry forward the line.

TABLE 7

Distribution of the plants of brevistylis through 5 generations, grouped as to the percentages of long-styled flowers.

PERCENTAGES IN CLASSES	GENERATIONS				
	First	Second	Third	Fourth	Fifth
0–10	.....	3	2	.....	1
11–20	.....	5	3	2	3
21–30	.....	6	3	.....	1
31–40	.....	7	.....	.....	1
41–50	.....	3	.....	.....	.....
51–60	1	2	1	.....	.....
61–70	1	4	1	.....	.....
71–80	2	3	.....	.....	.....
81–90	2	.....	.....	.....	.....
91–100	2	.....	.....	.....	.....
	8	33	10	2	6

Table 8 gives the comparative fertility of the plants selected as parents of the five generations of this selfed line of *brevistylis*. It presents a record consistent with that of table 7, showing that fertility fell off in the later generations as did the percentages of long-styled flowers. Thus the average number of seeds per capsule in those set by the five parent plants were 6.6, 13.0, 4.9, 3.0 and 2.6. The percentages of selfed capsules that set seed likewise declined with the later generations, e.g., 35.7, 57.1, 45.8, 23.8 and 28.0. The percentages of germination fluctuated without apparent significance. These conclusions, because of the very low fertility, are necessarily based on a small amount of data, but it is a matter of interest that they show a close correlation between higher degrees of fertility and higher percentages of long-styled flowers.

TABLE 8

Comparative fertility of the plants selected as parents of the five generations of this selfed line of brevistylis.

SELECTED PLANT	NUMBER OF FLOWERS SELFED	NUMBER OF CAPSULES THAT SET SEED	TOTAL NUMBER OF SEEDS	PERCENTAGE OF SELFED CAPSULES THAT SET SEED	AVERAGE NUMBER OF SEEDS PER CAPSULE	PERCENTAGE OF GERMINATION
Parent plant of the selfed line 15.15d, I–1	14	5	33	35.7	6.6	48.5
From first generation 16.2d, IV–4	14	8	104	57.1	13	34.6
From second generation 17.2, V–1	24	11	54	45.8	4.9	20.4
From third generation 19.2, I–3	21	5	15	23.8	3	26.7
From fourth generation 20.2–1	25	7	18	28	2.6	36.4

Thus after a five-years study of a selfed line of *brevistylis* I am brought to the conclusion that the factors which are responsible for the reduced style length and stigma structure in this plant, and with the correlated very low fertility, are fixed, in the sense that they express themselves through fluctuations within distinctly limited ranges. The lower ranges are close to the usual conditions in the plant, which are those of complete or almost complete sterility. The higher ranges may be found by close observations on performance and tests for fertility. They express a small but definite advance in style length and stigma structure and in somewhat increased fertility, but there is no evidence that such improvement will be inherited. Selections for increased style length and increased fertility failed to hold the gains and the results were so discouraging to further attempts to improve style length and fertility that this selfed line will not be continued.

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THE INTENSITY OF LINKAGE BETWEEN THE FACTORS FOR SUGARY ENDOSPERM AND FOR TUNICATE EARS AND THE RELATIVE FREQUENCY OF THEIR CROSSING OVER IN MICROSPORE AND MEGASPORE DEVELOPMENT[1]

WILLIAM H. EYSTER

University of Missouri, Columbia, Missouri

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TABLE OF CONTENTS

INTRODUCTION 597
Linkage intensity between the factor pairs S_u s_u and T_u t_u in maize 598
The relative frequency of crossing over between S_u s_u and T_u t_u in megaspore and microspore development 599
SUMMARY 601
LITERATURE CITED 601

INTRODUCTION

In a previous paper (EYSTER 1920) concerned with the linkage relations of the factors for sugary endosperm and the tunicate character in maize, data were presented which show a linkage between the factor pairs S_u s_u and T_u t_u, with an average crossover value of 29.15 ± 0.89 percent. A striking feature of these data was that crossing over seems to have occurred about eight percent more frequently in microsporogenesis than in megasporogenesis.

A statistical study of BREGGER's (1918) data on the linkage between the factor pair for waxy endosperm, W_x w_x, and the C c aleurone factor pair shows a similar but much less marked difference in the amount of crossing over in the production of microspores and megaspores. GOWEN (1919) pointed out that ALTENBURG's (1916) data on the linkage of factors in *Primula sinensis* show that crossing over also occurred more frequently in microspore development than in megaspore development.

In order to obtain more critical evidence on the relative amounts of crossing over in the formation of microspores and megaspores, individual

[1] The original crosses and back-crosses were made at CORNELL UNIVERSITY. I am indebted to that institution and especially to Dr. R. A. EMERSON for garden space and facilities for making the pollinations. The remainder of the work was done as a project of the Department of Field Crops, UNIVERSITY OF MISSOURI.

F_1 plants heterozygous for sugary endosperm and tunicate ear were crossed reciprocally with sugary non-tunicate plants. In the present paper are given the results obtained in the progenies of the reciproçal back-crosses.

EMERSON and HUTCHISON (1921) presented extensive data on the relative frequency of crossing over in microspore and megaspore development in maize. Their data include observations on factor linkages in two different chromosomes. The factor pairs *B b* and $L_g\ l_g$ are in the same chromosome and about 37 units apart. Crossing over between these factor pairs was found to have occurred, on the average, 1.43 ± 0.72 percent more frequently in microspore development than in megaspore development. This difference is small and probably not significant. The factor pairs *C c* and $S_h\ s_h$ are located in another chromosome at loci which are approximately 3 units apart. In this chromosome crossing over between *C c* and $S_h\ s_h$ was found to have occurred somewhat more frequently in megaspore development than in microspore development. From these data it was concluded that crossing over in maize is not greatly different in megaspore and microspore development.

LINKAGE INTENSITY BETWEEN THE FACTOR PAIRS $S_u\ s_u$ AND $T_u\ t_u$ IN MAIZE

A summary of the data previously reported on the linkage relation between the factors for sugary endosperm and tunicate ear in maize follows:

Non-crossovers		*Crossovers*		*Total*	*Crossovers*	*Percent crossovers*
$S_u\ T_u$	$s_u\ t_u$	$S_u\ t_u$	$s_u\ T_u$			
430	406	175	169	1180	344	29.15 ± 0.89

These back-cross data represent a coupling series as the constitution of the parents in the original crosses was $\frac{S_u\ T_u}{S_u\ \ t_u}$ and $\frac{s_u\ t_u}{s_u\ t_u}$, respectively.

In table 1 are given additional back-cross data on the frequency of crossing over between the factors $S_u\ s_u$ and $T_u\ t_u$. These data represent a repulsion series. The constitution of the parents in the original crosses were $\frac{s_u\ T_u}{s_u\ t_u}$ and $\frac{S_u\ t_u}{S_u\ t_u}$, respectively. A summary of the data recorded in table 1 follows:

Non-crossovers		*Crossovers*		*Total*	*Crossovers*	*Percent crossovers*
$S_u\ t_u$	$s_u\ T_u$	$S_u\ T_u$	$s_u\ t_u$			
1343	1121	547	433	3444	980	28.46 ± 0.52

These results are in close agreement with the data previously reported as may be seen by comparing the summaries given above. There is a difference of only 0.69 ± 1.03 percent.

TABLE 1

Frequency of crossing over between $S_u\ s_u$ and $T_u\ t_u$ observed in the back-crosses

$$\frac{s_u\ T_u}{S_u\ t_u} \times \frac{s_u\ t_u}{s_u\ t_u} \text{ and } \frac{s_u\ t_u}{s_u\ t_u} \times \frac{s_u\ T_u}{S_u\ t_u}.$$

PEDIGREE NUMBERS	$S_u\ T_u$	$S_u\ t_u$	$s_u\ T_u$	$s_u\ t_u$	TOTAL	CROSS-OVERS	CROSSOVER PERCENTAGE
1544–1545	45	145	144	51	385	96	24.94
1546–1547	23	84	53	32	192	55	28.65
1548–1549	40	104	96	25	265	65	24.53
1550–1551	25	62	52	29	168	54	32.14
1552–1553	55	84	38	32	209	87	41.63
1554–1555	27	65	53	24	169	51	30.18
1556–1557	55	167	125	46	393	101	25.70
1558–1561	81	163	148	44	436	125	28.67
1562–1563	32	66	66	16	180	48	26.67
1564–1565	37	96	89	24	246	61	24.80
1566–1567	37	93	67	37	234	74	31.62
1568–1569	60	117	97	25	299	85	28.43
1570–1571	30	97	93	48	268	78	29.10
Total	547	1343	1121	433	3444	980	28.46 ± 0.52

Following is a summary of the data on the linkage between $S_u\ s_u$ and $T_u\ t_u$, including both the coupling and repulsion series:

Non-crossovers	*Crossovers*	*Total*	*Percent crossovers*
3300	1324	4624	28.63 ± 0.45

The average crossover value is thus seen to be 28.63 ± 0.45 percent.

THE RELATIVE FREQUENCY OF CROSSING OVER BETWEEN $S_u\ s_u$ AND $T_u\ t_u$ IN MEGASPORE AND MICROSPORE DEVELOPMENT

As already indicated F_1 plants of the constitution $S_u\ s_u\ T_u\ t_u$ from the cross $\frac{s_u\ T_u}{s_u\ t_u} \times \frac{S_u\ t_u}{S_u\ t_u}$ were back-crossed reciprocally with non-tunicate plants having sugary endosperm. The results are listed in table 2. When the F_1 plants were used as seed parents the percent of crossing over varied from 26.67 ± 2.28 to 32.14 ± 2.36. When the same F_1 plants were used

TABLE 2

Crossing over between S_u s_u and T_u t_u as shown by the back-crosses

$$\frac{S_u\ t_u}{s_u\ T_u} \times \frac{s_u\ t_u}{s_u\ t_u} \text{ and } \frac{s_u\ t_u}{s_u\ t_u} \times \frac{S_u\ t_u}{s_u\ T_u}.$$

PEDIGREE NUMBERS	F1 PLANTS AS SEED PARENT							F1 PLANTS AS POLLEN PARENT								
	Su Tu	*Su tu*	*su Tu*	*su tu*	TOTAL	CROSS-OVERS	CROSSOVER PERCENTAGE	*Su Tu*	*Su tu*	*su Tu*	*su su*	TOTAL	CROSS-OVERS	CROSSOVER PERCENTAGE	DIFFERENCE	DIFF. / P.E.diff
660–13	27	65	53	24	169	51	30.18±2.35	100	312	269	97	778	197	25.32±1.10	−4.86±2.59	1.88
660–16	32	66	66	16	180	48	26.67±2.28	81	163	148	42	434	123	28.34±1.47	+1.67±2.71	0.62
661–2	25	62	52	29	168	54	32.14±2.36	55	84	38	32	209	87	41.63±2.12	+9.49±3.17	2.99
663–6	60	117	97	25	299	85	28.43±1.77	30	97	93	48	268	78	29.10±1.87	+0.67±2.57	0.26
663–9	37	93	67	37	234	74	31.62±2.01	37	96	89	24	246	61	24.39±1.95	−7.23±2.80	2.58
Total	181	403	335	131	1050	312	29.71±0.95	303	752	637	243	1935	546	28.22±0.98	−1.49±1.36	1.10

as pollen parents the percent of crossing over varied from 24.39 ± 1.96 to 41.63 ± 2.12. A summary of these data follows:

	F_1 as seed parent	F_1 as pollen parent
Non-crossovers	738	1389
Crossovers	312	546
Total	1050	1935
Percent crossing over	29.71 ± 0.95	28.22 ± 0.98
Difference $= 1.49 \pm 1.36$;	$\frac{\text{Diff.}}{\text{P. E.}_{\text{Diff.}}} = 1.10$;	$P = 45.81$

In megaspore development the average percent of crossing over was 29.71 ± 0.95 while in microspore development it was 28.22 ± 0.98. From these results it is to be concluded that crossing over in these five F_1 plants occurred on the whole 1.49 ± 1.36 percent more frequently in megaspore development than in microspore development. A deviation as large as this would be expected to occur about once in every two trials due to the errors of random sampling.

SUMMARY

A total of 4624 back-cross plants, representing both coupling and repulsion series of the factor pairs S_u s_u and T_u t_u, have been observed. The average percent of crossing over between these factor pairs was found to be 28.63 ± 0.45.

The same F_1 plants were used both as seed and as pollen parents in back-crosses with double-recessive plants to determine the relative frequency of crossing over in megaspore and microspore development. It has been found that crossing over between S_u s_u and T_u t_u is variable in both megaspore and microspore development and occurs in each process with approximately the same frequency. This is in agreement with the conclusion reached by EMERSON and HUTCHISON (1921) in their study of the relative frequency of crossing over in megaspore and microspore development in maize.

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INDEX

Prepared by DR. J. BEN HILL of the Botany Department, THE PENNSYLVANIA STATE COLLEGE, State College, Pennsylvania and Mrs. HELEN DEUSS HILL. Page numbers printed in black-faced type refer to headings of articles or of sections. Numbers in italics indicate references included in lists of "Literature cited."

Acer Pseudoplatanus 569
ADKINSON, JUNE 576, *581*
Alcohol and fertility of white rats **117**–141
Alcohol
  As selective agent 134
  Effect of genetically 139–141
  Eliminating germ cells or zygotes 140
  Reduces number of young 139
Alcoholism and the growth of white rats **427**–444
  Administration of alcohol by inhalation 428
  Alcohol as selective agent upon genetic differences 428
  Alcohol effect of fumes on treated animals and descendants 427
  Alcohol effect on growth of rats, 438, 440, 441, 444
  Alcohol effect on weight 442-443
  Alcohol prevents reproduction 444
  Alcohol reduces rate of growth 440, 441, 444
  Alcohol treatment retards growth of rats 438
  Differences between weights of tests and controls 433
  Effects of alcohol 443
  Frequency distributions of weights of treated males at different ages 436
  Growth curves of test and control females 437
  Methods of experimentation **428**–431
  Offspring of treated rats genetically superior to controls 441
  Offspring of treated rats heavier than controls 439, 440, 444
  Offspring of treated rats more fecund than controls 431
  Rats, growth retarded by alcohol treatment 438
  Selective effect of alcohol on rats 440, 441
  Treated females less often pregnant than controls 431
  Treated males grow less rapidly than controls 435
  Treated rats less fecund than controls 431
  Weight data from treated males 435
  Weight per female rat 432–433
  Weight per male rat 430–432
ALDER, B 274, 275, 277, *317*
ALDROVANDUS 466
ALLEN, E 517, *550*
Allergic conditions 581
Allogamous population, selection in **508**–512
ALTENBURG, E. 386, *425*, 597, *601*
Andromonoecious types of maize **203**–236
Angioneurotic Edema **573**–582
  Anaphylaxis 579
  Causes 573–574
  Cross of affected×unaffected 577
  Description 573, 576
  Edema of the glottis 577
  Factors possibly two in inheritance 580
  Familial **577**–581
  Heritable 574
  Inheritance explanation 580
  Parents neither affected 579
  Sporadic **575**
ANONYMOUS 466, *506*
Anther ear type of maize **203**–236
Aphis avenae, selection ineffective 143
Arcella 144, 176, 181
Arenga saccharifera 150
ARLITT, A. H. 428, 441, *444*
Ascomycetes 149
Ascus stage of fungi imperfecti 149
Assortment, independent 397
Asthma 575, 581
  Heredity 576
  Recessive 576

BABCOCK, E. B. 338, 535, *550*
BALL, E. D. 274, 275, 277, *317*
BALLY, W. 514, *550*
BAILEY, I. W. 517
BAILLY-MAITRE, J. 467, 473, *506*
BARBER, M. A. *182*
Bar-eye a sex-linked character 5
Bar-eye not fully dominant 5
Bar-eye, origin in *Drosophila melanogaster* 5
BARROWS, WILLIAM MORTON **573**–582
Bars in pigeons **466**–506
BARTLETT, H. H. 146, 147, *183*, 545, *552*
BATESON, W. 545, *550*
BAUR, P. 333
BELLING, J. 526, 528, 532, 545, *550*
BENEDICT, F. G. 272, *273*
Bigenic character, determination of loci 407
Bigenic hypothesis 387, 391, 392, **397**–400
Bigenic nature of ski in *D. melanogaster* **391**–394, 399
Biometric studies of variable groups 182
Black in pigeons **466**–506
BLACKBURN, K. B. 532, *550*
BLAKEMAN, J. 280, *317*
Blakeslee, A. F. 275, 302, 303, 307, 308, *317*, 446, 447, 451, 452, 455, 463–*465*
BLARINGHEM, L. 203, *226*
BOITARD 467, 498, *506*

Bolten, G. C. 577, *581*
Bonhote, J. L. 468, 475–477, *506*
Bouin (solution) 517
Boveri 523
Brachydactyly 585
Bravais 259
Bregger, T. 597, *601*
Breitenbecher, J. K. 484, *507*
Bridges, C. B. *334*, 338, 344, 355, 373, 376, *379*, *380*, 386, 389, 391, 394, 396, 397, 411, 412, 418, 419, *425*, 527, *550*
British Museum 467
Brown, Aaron 575, *581*
Bruchus 484
Bud mutations associated with tetraploidy 543
Buffon, Count de 466, *507*
Bulloch, W. 577, *581*
Bursa 530
Bussey Institution of Harvard Univeristy 237, 516

California, University of 389
Calliphora erythrocephala 588
Cameron, C. 577, *581*
Canna 532
Carbohydrate, a rare, in waxy maize **568**–572
Card, L. E. 317, 447, 452, 464, *465*
Castle, W. E. 543
Cataract 583
  In female line 584
Cattle dominant white 424
  Recessive albino condition 424
Causation and path coefficients **258**
Cell division in wheat species 544, 548
Centropyxis 144, 176, 181
Chapman, E. R. B. 472, 498, *507*
Characters arise by recombination 422
Characters, similar, conditioned by different genes 424
Checks in pigeons **466**–506
Chelidonium majus 569
Chromosome
  Abnormal and sterility 534, 540
  Behavior and sterility 533–540
  Behavior in partially sterile hybrids (see wheat) **513**–552
  Complex in Drosophila species 337
  Duplication 526
  Groups of, in various species of Drosophila 336
  Number and cell size correlated 519, 523, 540
  Number and size of pollen grains in wheat species 523–526, 549
  Number and sterility 534
  Number, doubling results in duplication of genetic factors 526–527
  Number in wheat 514–515, 525–526, 540–543, 547, 557
  Numbers in plants 526
  Ratios influence characters other than sex 527
  Rearrangement in Drosophila species 342
  X in *Drosophila obscura* longer than in other species 374
Chromosomes
  And linkage groups 341
  Assortment in polyploid species 527–530
  Behavior in reduction divisions of species of Rosa 531
  Complete set necessary for gametic and somatic development 537
  Five pairs in *Drosophila obscura* 341
  In cultivated species of wheat **517**–521
  Of rye 519
  Reduplication does not cause sterility 534
  X of three Drosophila species, maps 375
  X parallelism 337
Chrysanthemum chromosome number 527, 545
Clausen, R. E. **385**–426, 424, *426*
Coca, Arthur F. 573, *581*
Cole, L. J. 468, 472, 473, 480, 502, 503, *507*
Collins, G. N. 568, 571, *572*
Collins, J. L. **385**–426, 535, *550*
Color in flowers effect of temperature on inheritance 333
Color patterns in doves corresponding to those in pigeons 502
Columba (see pigeons)
Columba affinis 471, 505
Columba guinea, 467, 502
Columba gymnocyclus 467, 505
Columba intermedia 494, 495, 505
Columba leuconata 467
Columba livia 467, 468, 494–496, 500, 502, 505
Columba oenas 472
Columba rupestris 467, 505
Columba schimperi 467, 505
Columbae 468
Columbia University 389, 391, 394, 396
Columbidae 467, **501**–502
Columbigallina rufipennis 502
Compound, defined 345
Connecticut Experiment Station 237–239, 255
Cooke, Robert A. 574, 576, *581*
Corbié 467, 498, *506*
Corn (see maize)
Cornell University 203, 559, 597
Correlation and path coefficients **258**–273
Correlation in hybrid sterility in wheat 514
Crepis chromosome number 526, 545
Crepis Reutreiana "*gigas*" *mutant* 526
Crepis tectorum×*Crepis virens* 535
Crepis virens 526, 535
Cromwell, Hobart *334*
Crossing over 373
  Correlated with cytological length of chromosome 374
  In Drosophila and change of temperature 338
  In maize **597**–601
  In sex-linked groups in *Drosophila obscura* 340–341
Crowder, Joseph Reed 577, 578, *581*
Crowder, T. R. 577, 578, *581*
Culms inheritance in maize **559**–567
Cunier 583
Cytological methods in wheat 517

DAFERT 569
Daltonism 583, 585, 588
DARWIN, CHARLES 467, 468, 471, 473, 480, 487, 495, 505, *507*
Datura, chromosome number 526, 528, 530, 532, 533
  New species 534
  Normal 534
  Poinsettia mutant 528
  Sterility 533
  Triploid 534
  Trisomic 534
DAVENPORT, C. B. 585, *589*
DAVIS, B. M. 530, 531, *550*, **590**–*596*, 591, 595
Deficiency in *Drosophila obscura* 355
DETLEFSEN, J. A. 424, *426*
Dextrins 568
Diandric heredity WZ type of sex linkage 583
Diagynic heredity XV type of sex linkage 583, 589
Didynium nasutum 144, 176, 181
Difflugia 144, 149, 157, 178, 181
DIGBY, L. 526, *550*
Diptera 372
Disease resistant races in maize 252
Dominance reversed 527–528
DORSEY, M. J. 542, *550*
Doves and pigeons, similar color patterns 502
Doves, species of 502
Drosera 531, 532
Drosophila 349
  Graded multiple-allelomorph series 504
  Intersex 527
  Interspecific crosses 376
Drosophila ampelophila 337
Drosophila funebris 351, 376
Drosophila hydei **319**–334
  Backcross ratios 324
  Backcross 325
  Combination of scarlet and variable under different temperatures **326**–330
  Crosses
    Backcross hybrid ♀ × variable scarlet ♂ 331
    Backcross variable scarlet ♀ × hybrid ♂ 331
    F_2 from normal-eyed variable scarlet ♀ × wild stock ♂ 329
    F_2 from wild stock ♀ × normal ♂ from variable 330
    F_2 from wild stock ♀ × speck-eyed scarlet ♂ 329
    F_2 from wild stock ♀ × variable scarlet ♂ with minimal eyes 329
    Normal-eyed ♀ from variable scarlet stock × wild stock ♂ 328
    Normal-eyed scarlet ♀ from pure minimal mass culture × wild stock ♂ 330
    Normal mahogany ♀ × variable scarlet ♂ 331
    Variable scarlet ♀ × normal mahogany ♂ 331
    Wild stock ♀ × minimal-eyed scarlet ♂ 329
    Wild stock ♀ × normal ♂ from minimal 330
    Wild stock ♀ × scarlet variable ♂ with normal eye 328
    Wild stock ♀ × variable scarlet with very small eyes 328
  Double recessive scarlet variable 324
  Environmental influence on mutant 325
  Environmental stimulus causing phenotypic differences 333
  Eye mosaics **333**
    Inheritance effect of environment 333
  Linkage 320
    Of variable and scarlet 319–320, **323**–325 331, 334
  Mahogany normal 331, 332
  Mahogany variable 331, 332
  Mosaic 333
  Mosaic male 333
  Mutant dependent on environment 319 322–330
  Mutant scarlet 321, 333
  Mutant "variable" 319
  No crossing over in the male 331
  Scarlet 320, 324, 330
    A new mutant eye color 320
    Normal 331, 332
    Variable 322, 325, 331, 332
      In reduced temperature 328
      In warm temperature 327
  Sex ratio 325
  Variable 324, 325, 333
    Behavior in inheritance **322**–323
    Dependent for expression on environment 334
    Is recessive 320
    Origin and description **321**–322
    Response to temperature 332, 333
    Reversion due to low temperature 332–333
    Scarlet 325
    Stock cultures 330–333
    Stock established by selecting variable eye **330**, 332
    Under controlled temperature 319, **323**
    Wing mutation in culture variable 330
Drosophila melanogaster 333, 337–340, **342**, **345**, 347, 351, 354, 355, 357, 359–361, 367–369, 374–379
  Abnormal abdomen 333
  Bar 391
  Bar-eyed mutant expression of temperature 333
  Black 397, 407
  California curled 389
  Club 388
  Curled 388, 389, 390
  Dichaete 386, 391, 397–399, 401, **402**, **413**–415
  Dominant mutant genes 400
  Duplex 413, 414
  Duplication 386
  Eosin eye color modifiers 386
  Eye color modifiers 504

Drosophila melanogaster (continued)
Eye facet number expression of temperature 333
Genes, modifying 386
Inheritance of ski wings 385–426
Jaunty 388–390
Lethals balanced 386
Mutation by recombination 423
Mutation, point 423
Non-disjunction 386
Notch wings 386
Ratios wild type to ski 403–407
Sable 527
Scute 376
Selection in White Bar Eye 1–115
Bar eye 2, 3
Changing to full eye and ultra-bar 4
Coefficient of dominance 21
Facet number affected by temperature 3, 8
Factorial units 5
Low bar 22, 23
Not fully dominant 5
Origin 5
Red bar stock 7
Selection for high facet number 3, 114
Selections for low facet number 3, 114
Sex-linked character 5
Sex ratios affected by lethal mutant factors 70
Sexual dimorphism 6–7, 92
Change in 70
Stock 2, 5–7
Germinal diversity 2
Ultra-bar 16, 22, 114
Vestigial-winged bar 3, 7
White bar-eye race 1–115, 7
Class facet values 15, 20
Correlation between degree of selection and effectiveness 107–112
Crosses
Between high and low lines 3
Ultra-bar×bar 24, 28
Dominance of bar and full 21
Facet and factorial values of selected pairs for all matings 32–44
Facet differences not of hereditary value 112
Facet factors eliminated by selection 4, 114
Facet number affected by sex-linked lethal factor 86, 113–115
Facet number conditioned by elimination of factors 86
Facet number factors environmental effect 14–16
Facet number factors germinal effect 14–16
Facet number inhibitor 16
Facet number 26
Factorial values for facet number 13, 15, 20
Factorial values frequencies 54–69, 71–78
Formula for coefficient of dominance of bar-eye 21
Full eye 4, 22–23, 112, 114
Facet number 5
Germinal differences 84, 88
Arise by mutations independently of selection 113, 115
Heterozygosity effect in bar eye 84
Low-selected bar 16
Means, female and male 92–103
Mutants to full eye and to ultra-bar 49, 112, 114–115
Mutation to full eye from selected bar 84, 112
Mutations independent of selection 114
Non-heritable fluctuations 84
Ontogenetic development of characters 2
Pedigrees in high line 10
Pedigrees in low line 9
Restriction in range, selection in bar eye 84
Rudimentary 5
Selected lines of bar-eye range 78–87
Selection
Bar eye matings in 8
Bar eye original data 24
Effect due to elimination of germinal groups 78–87, 113
Effect on females 45, 113
Effectiveness 112, 113
Difference between parent and offspring 95–98
Eliminating facet factors 4
For eye facet number 1–115
Germinal changes 2
In bar eye temperature control 8
Lines, low and high compared 24, 25
Methods 7–12
On basis of performance 88
Positive results by conserving mutation 4
White bar 12, 19–21, 26
High selection 27, 30, 47–48, 52–69, 91, 92, 114
Low and high lines contributions to divergence 91–92
Low and high lines differences 88–91
Low selection 26, 27, 29, 45–46, 50–51, 54–69, 92, 114
Selections eliminating germinal factors 112
Sex-linked lethal factor 92
Standard deviation 99, 104–106
Synchrony between low and high generations 12
Temperature effect 16
Ultra-bar mutants 85, 112–114, 115
Unselected bar 16
Variability in ultra-bar bar and full eye 22
Sepia 393, 397, 405
Sepia locus 396
Sex-linked jaunty 389
Ski 398–400, 402, 407
Ski-II 385
Determination of locus 407–412
Ski-III 385

Drosophila melanogaster (continued)
Determination of locus **413–420**
Ski **385–426**
Bigenic character 387, 399, 407, 425
Bigenic hypothesis 387, 391, 392, 393, **397–400**
Bigenic nature 388, **391–394**, 399
Characters employed in analysis **396–397**
Chromosome position 393
"Crimp" in costa or marginal vein 390
Description **389–390**
Differs from wild type in two pairs of genes **400**
Duplex 389, 392, 393, 398, **400–403**, 413
Examination of flies 396
Experimental methods **394–396**
For instructional purposes 421
Genotypes 392
Inheritance 424
Linkage relations 393
Locus 388
Maintaining stocks 395
Mode of inheritance 424
Not a monogenic character 399
Origin and history **387–389**
Procedure with experimental cultures 395
Ratios wild to ski **403–407**
Recombination in connection with origin of 422
Resembles jaunty and curled 388, 389
Reversion to wild type 388
Segregation 393
Simplex 392, 394, **400–403**, 404
Morphological differences from duplex flies 403
Mated *inter se* 403, 404
Phenotypically identical with jaunty 389
Star ski **398–401**, 407, 414
Technique of breeding **394–396**
Types of reciprocal matings 392
Variable in expression 389
Spineless 397, 413
Spines number 386
Star **391**, **396–402**, 407, 414
Star black **407**
Star dichaete **397–402**, 413
Streak 386
Truncate wings 386
Vermillion 377, 527
Vestigial modified by differences in temperature 333
Vortex 386
White 358
White-eyed males 387
Wild type constant **385–386**
Drosophila mulleri 321
Drosophila obscura **335–384**, 387
Allelomorphic series, white and eosin multiple 359
Autosomal characters 357
Bithorax 357
Chromosome
Genetic length 340
Localization of genes **348**
Long 341
Map **373–374**
Involving beaded, vermilion, fused and short 349
Rearrangement 342
X, loci in 384
X very long 379
Chromosomes, five pairs 341
Crosses
Glazed×beaded **364**
Glazed×pointed **364**
Miniature×fused 368
Miniature×vermilion 368
Notch×reduced rough 354
Pointed×beaded 362, 363
Polished×rough 371
Reduced rough×vermilion 350, 371
Singed male×fused short female 369
Singed×yellow vermilion 370
Vermilion×beaded 348
Vermilion×short 348
Crossovers between
Ascute with pointed and yellow 367
Beaded-vermilion-fused and short **348**
Compressed and fused 367
Glazed and beaded 364
Miniature and reduced 369
Notch and reduced 354
Notch and shorter 352
Reduced and rough 351
Scutellar and yellow 361
Vermilion and broken 365
Vermilion and reduced 354, 369
Vermilion beaded and short 348
White and fused 370
White and notch 358
White and singed 369
Crossing over between sex-linked characters **339–341**
Crossing over in X chromosome 379
Culture methods **338**
Deficiency 355
Difference in sequence 360
Dominance relations of short allelomorphs **344**
Genes, order 348
Genes, sequence 351, 359, 360, 379
Lethal factors 372
Lethal, notch 351
Linkage experiments **382–383**
Linkage groups 339, 341
Linkage of
Compressed and fused 367
Dwarf and short 371
Glazed and fused 363
Rough and fused 351
White and yellow to notch 358
Yellow and notch to eosin 359
Linkage relations of sex-linked characters **335–384**
Loci of reduced and rough **350–351**
Loci of yellow, notch and white or eosin **359–360**

Drosophila melanagaster (continued)
Modifying factor 335, **342**–345
Multiple allelomorphic locus 335, **342**–345
Mutability 335, **339**
Mutants
Achaete modifier 335, **355**
Achaete notch 356
Ascute 336, 367, 378, 381
Between fused and short 367
Locus 367
Beaded 335, **345**, 347, 361, 362, 363, 373, 381
Locus and valuation **346**, 374
Broken 336, **347**, **364**, 381
Dominant in females 364, 365
Lethal in male 364
Locus **365**
Sex-linked recessive lethal 365
Compressed 336, 350, **366**, 374, **378**, 381
Locus **367**
Deformed 336, **371**, 381
Lacking in vigor 372
Dwarf 336, **371**, 381
Eosin 336, 342, 354, **358**, **359**, 376, 381
Extended 336, **372**, 381
Lacking in vigor 372
Fused 335, **346**, 347, 363, 370, 373, 381
Locus 374
Gap 335, **344**
A modifier of short 344–345
Glazed 336, 350, **363**, **377**, 381
Homozygous females sterile 363
Locus **363**
Grooveless 367
Lethals 381
Miniature 336, **368**, 370, 371, **377**, 381
Locus **368**
Minus, autosomal 349
Minute 356
Notch 335, 342, **351**, **352**, 361, 381
Deficiency nature **354**
Locus **353**–354
Recessive lethal 351
Similarity to notch mutants in other species 351
Specific notch modifiers **355**
Notch$_2$ 335, **352**, 355
Notch$_3$ 335, **353**
Pointed 336, **361**, 362, 367, 381
Locus **362**
Polished 336, **370**, 371, 381
Locus **370**
Reduced 335, **349**, 350, 354, 371 381
Rough 335, **350**, 354, 381
Nature and cause of character 350
Scutellar 336, 355, **360**, 376, 381
Locus **361**
Short 335, **342**, 347, 363, 381
Shorter 335, **343**, 381
Shortest 335, **343**, 381
Singed 336, **369**, 371, **377**, 381
Females sterile 369
Locus 369
Slender 336, **365**, 381
Locus **366**
Split 356
Modifier of notch 335, **356**
Notch$_2$ 356
Stubby 336, **372**, 381
Vermilion 335, **347**, 362, 364, 370, 371, 374, **377**, 381
White 335, 342, 347, 353, 354, **357**, **359**, 369, 370, **376**, 381
White$_2$ 336, **357**
Yellow 335, 342, 353–357, 361–363, 367, 370, 371, 373, 374, **376**, 381
Notch combination 353
Mutants similar to those of other species and corresponding chromosome regions **375**
Mutation, frequent in middle region of X chromosome 347
Mutations identical with those in other species 339, 379
Mutations in X chromosome 378
Non-disjunction of sex chromosomes not found 339, 340
Scarlet 357
Sex-linked characters description and location **342**–373
Sex-linked group compared with other species of Drosophila 373
Slender-bristle stock 356
Vermilion and broken crossovers 365
Vermilion and reduced Broken crossover 365
X chromosome includes a region not present in X chromosome of *D. melanogaster* 339
Drosophila repleta **319**, 320, 321
Eye color mahogany 322
Seven modifiers acting on eye color 504
Sex determined by ratio of X chromosomes to autosomes 527
Sex-linked mutant 320
Drosophila simulans 337, 347, 377
Sterile F_1 535
Drosophila species forked 372
Drosophila superiority for genetic investigation 425
Drosophila virilis 337, 347, 374, 375, 377–379
Drosophila willistoni 377
Drosophilae 321
DUDLEY, A. H. 514, *550*
Dwarf type of maize **203**–236

EAST, E. M. 203, 219, *226*, 237–240, 248, 250–252, 254, *257*, 514, 517, 527, 539, 540, 542, 545, *550*, *551*
EATON, J. M. 467, *507*
Eczema 575, 581
Edema of the glottis 573, 577
EDGERLY, EDWARD T. 577, 579, *581*
EGBERT, A. D. 274, 275, 277, *317*
Egg Production in fowl **274**–318
Egg production in Rhode Island Red breed of domestic fowl **446**–465
Biological factors on which fecundity depends 447

Egg production in Rhode Island Red breed of dometic fowl (*continued*)
Correlation between annual production of deviation of individual months **455–457**, **464**
Correlation between individual months and annual production **448–454**, **455–457**, 464
Correlation between records of individual months of same year **457–463**, 464
Correlation of individual month and other eleven months **454**, 455
Correlations of egg production of Rhode Island Red agree with those for White Leghorns 465
Distribution of magnitudes of correlations between individual months and
Antecedent months 461
Subsequent months 460
Physiological activities at various periods interrelated **446**
Regression equations for prediction of annual egg production 450
Regression of annual production on monthly production 451–453
ELDERTON, W. P. *317*
EMERSON, R. A. **203–236**, 210, 219, *226*, 559, 560, *567*, 597, 598, *601*
EMERSON, STERLING H. **203–236**
Endosperm development and F_2 sterility in wheat **553–558**
Endosperm formation not due to triploid condition 558
ENRIQUES, PAOLA **583–589**
Epistatic series in pigeons **480–487**, 499, 500, 502, 503
Erythrodextrin 568–570
Occurrence in plants 569–570
Evolution
By hybridization 422–424
By mutation 182
By selections of fluctuating variations 182
EWING, H. E. 143, *182*
Eye color, mahogany in wild type *Drosophila repleta* 322
Eye selection 330, 332
Eyeless mutant in *Drosophila hydei* **319–334**
EYSTER, W. H. **559–*567*, 597–*601***

Factors presence and absence theory 424
FARNHAM, M. E. 526, 528, *550*
Fecundity dependence on biological factors 447
FEDERLEY, H. 532, *550*
Fertility of rats treated with alcohol 440
Fertility of white rats, influence of alcohol **117–141**
Fertility reduced by alcohol treatment 139
FIELD COLUMBIAN MUSEUM 467, 506
Fleming solution 517
Fowl, correlation between first and second year egg production **274–318**
Annual egg production 307
Anatomical fecundity 276
Autumn production 299, 302
Barred Plymouth Rock 276

Color criteria in egg production 275
Condition of birds with respect to laying activity 302
Correlations between
Annual production for two years 281
Egg production of first and second year **274–318**, 276, 280, 283, 294, 305, 313, 314, 316
First and third year 277
Individual months of first two years **290**, 291
Individual months of first and second year 285, 287, 294, 296
Individual months of second year and first year 286
Inter-annual 311
Inter-annual for monthly production **287–293**, 296, 297
Genetic significance **293–302**
Inter-annual for "cycles" of first and second year 299
Inter-annual for various months of first and second year 284
Inter-annual of flock, means **283–284**
Monthly records of one year and annual record of another year **284–287**
Second and third year 277
Summer months of first year and winter months of second year, low 298
Summer months of first year and months of various periods of second year 298
Winter months of two years 294
Correlation, intensity between two years 301
Correlation significance of deviation 301
Correlations, summary of data 300
Criteria in egg production 275
Cycles 296, 297
Egg production
Color criteria 275
First and second year 308–310
Inter-annual correlation 275, **278–280**
Primary factor 282
Mean annual 281, 306
Seasonal distribution 277
Fecundity of diverse periods 275
Fertility dependent on Mendelian factors 293
First year production, mean 278, 303, 304
Individuality of the bird 282
Inheritance of fecundity 274, 275
Linearity of regression in egg production 280, 286
Mean production of first and second years correlated 314, 315
Mendelian factors for winter production 293
Not differentiated by summer and autumn production 300
Production lower second year than first year 305
Ratios of correlation coefficients to their probable errors 290, 292
Records by months 311–313
Records, egg production of first and final

Fowls (*continued*)
months of first year related to second year's record 310
Regression equation in egg production 279, 287
Regression linearity in egg production 280, 286
Regression of second-year annual production on first year monthly production 288, 289
Second-year egg production, mean 278, 279, 303–305
Selection, basis 305
Spring production 299
Spring or reproductive cycle 293, 294, 300
STORRS INTERNATIONAL EGG-LAYING CONTEST 302–308
Summer production 299
VINELAND INTERNATIONAL EGG-LAYING AND BREEDING CONTEST 277, 282, 304–308, 314
White Leghorns 276, 277, 302, 316
Heritable differences 300
Winter cycle of egg production 293, 294, 300
Winter production of first and second year 293
Winter production 299, 302
Fowl
Domestic, egg production 446–465
Treated with alcohol, growth curves 443
Fowls
Domestic, Silky, White Leghorns, White Plymouth Rock, White Wyandotte, 424
Treated with alcohol and ether, fertility data 137, 138
Whites dominant 424
Whites recessive 424
FREUDENTHAL, WOLFF, 576, *582*
Fungi Imperfecti 142, 145, 149

GAINES, E. F. 530, 535, 538, *551*
Gallus (see fowl)
GALTON, FRANCIS 259, *273*
Gametophytic characters controlled by sporophyte 547
Gametophytic chromosomes control of characters by 547
GARBER, R. J. 238, 239, 251, *257*
GATES, R. R. 527, 530, 531, 534, *551*
GAUSS 259
GEERTS, J. M. 531, *551*
Gene, change in composition 424
Genes, different conditioning similar characters 424
Genetic differences, effect of alcohol on 428
Genetics of maize 237, 238
Gentiana lutea 569
Geopelia striata 502
Germ-cells eliminated by alcohol 134, 140, 141
Germ-cells inferior eliminated by alcohol 134
Germinal differences in *Drosophila melanogaster* 84
Germinal modification due to alcohol 139, 140
GHIGI, A. 505, *507*
GIBSON, W. 280, *317*
GOODALE, H. D. 446–*465*, 447
GOODSPEED, T. H. 424, *426*
GOWELL, G. M. 275, 276, *317*
GOWEN, J. W. 419, *426*, 597, *601*
GRANDIDIER 583, 585
GREGORY, R. P. 528, *551*
GRIFFEE, FRED 239
GRIS 569
Growth factors in maize 220, 221
Guinea pig 264–268
Birth weight 265, 266
Drunken by inhalation 123
Fatally affected by large doses of alcohol 136
Genetically selective action of alcohol 139
Gestation period 264, 266
Litter size 126, 264–266
Prenatal growth curve 265
Rate of growth 266
Reduction of litters by alcohol 135

HAGEDOORN, A. L. 422, *426*
HAGEDOORN, VORSTHEUVEL LA BRAND, A. C. 422, 426
Haidenhain (iron-haemotoxylin) 517
HANEL, ELISE 143, *182*
HANNAS, RALSTON R. 277, *317*
HARPER, R. A. 571, *572*
HARRIS, J. ARTHUR 143, *183*, 270, 272, *273*, 274–318, 275, 281, 301–303, *317*, 446–465, 451, 452, 455, 457, 463, 464, *465*
HARRISON, J. W. H. 532, *550*
Hay-fever 575, 581
HAYES, H. K. 203, *226*, 237–*257*, 238, 251, 527 536, *551*
HEGNER, R. W. 144, 176–179, 181–*183*
Helminthosporium 182
Hemerolopia 588
Hemophilia 583, 585, 588
In the female line 584
Heredity
Hologynic, a new type 583, 589
Of angioneurotic edema 573–582
Heritable characters, methods of modifying and controlling 427
Heterozygosity effect on bar eye in Drosophila 84
Hevea brasiliensis 168
Hexaploid forms 526
Hexaploidy in wheat species, origin of 540–541
Hieracium auricula×*H. aurantiacum* 531
Hieracium chromosome number 526, 532
Hieracium excellens 531
High protein maize produced by Mendelian methods 237–257
VAN'T HOFF 16
HOGE, MILDRED A. 333, *334*
Holoandric heredity, through male line 583, 589
Hologynic heredity 583–589
Explanation 586–587
Hemophilia 584
Heredity through female line 583
Known only in man 589
Selective fertilization 587, 588
Senile cataract 584
Sex-linked characters 583

HOWARD, A. 530, *551*
HOWARD, G. L. C. 530, *551*
HORTON 254, 255
Human basal metabolism 272
  Body surface 272
  Body weight 272
  Correlation coefficients 272
  Heat produced 272
  Hereditary and environmental factors 272
  Path coefficients 272
  Stature determines body surface 272
  Stature determines body weight 272
HUTCHISON, C. B. 598, *601*
Hybrid vigor effect 533
Hybrids, sterility in wheat **553**–558
HYDE, ROSCOE R. **319**–334, 320, *334*
Hydra selection not effective 143

INDIANA UNIVERSITY 568
Inheritance
  Modified by temperature in Drosophila 333
  Of fecundity in fowl 274
  Of ski wings in *Drosophila melanogaster* **385**–426
  Of zigzag culms in maize **559**–567
INTERNATIONAL EGG LAYING CONTEST 448, 451
Iris germanica 569

JENKINS 239
JENNINGS, H. S. 142, 144, 157, 174, 178, 179, 181–*183*
JOHANNSEN, W. 142, 143, 175, 181, *183*
JOHNS HOPKINS UNIVERSITY 258
JONES, D. F. 238–240, 248, 250–252, 254, 255, *257*, 571, *572*
JONES, SARAH VAN HOOSEN **466**–506

KAUFFMAN, C. H. 150, *183*
KELLEY, FRANK J. 469, 486, *507*
KEMPTON, J. H. 203, *226*, 569, 570, 571, *572*
KIHARA, H. 514, 515, 537, 539, 540, *551*
KIRKPATRICK, W. F. 275, 302, 303, 307, 308 *317*, 446, 447, 451, 452, 455, 463, *465*
KÖRNICKE, M. 514, *551*
KRAFKA, JOSEPH, JR. 1, 3, 8, 12, 13, 16, 17, *115*, 333, *334*
KURTZWEIL, C. 536, *551*

LARUE, CARL D. **142**–201, 146, 147, 168, *183*
LANCEFIELD, D. E. **335**–384, 345, 372, *379*
LASHLEY, K. S. 143, 144, *183*
Lepidoptera 587
Lethal factors in *D. obscura* 372
LEWIS, HARRY R. **274**–318, 277, 303, *317*, 447, 457, *465*
LIEBIG 168
LINDSTROM E. W. 560, 565, *567*
Linkage in *Drosophila hydei* 320
Linkage in maize 560, **565**, **597**–601
Linkage relations in *Drosophila obscura* **335**–384
Litters, number compared in guinea-pig and rat treated with alcohol 137
LOTSY, J. P. 422, *426*

LUSK, FRANK B. 577, 579, *581*
LUTZ, A. M. 526, *551*
LYELL, J. C. 473, 487, *507*

MACDOWELL, E. C. **117**–*141*, 122, **427**–445, 428, 431, 435, 440, *444*
MCCLUNG 517
MAINE AGRICULTURAL EXPERIMENT STATION 516
Maize
  Aleurone color 424
  Andromonoecious type recessive to monoecious 203
  Andromonoecious types **203**–236, 225
  Anther ear type **203**–236, 207, 222, **224**–225
    Characteristics **204**–210
    Double recessive 207–210
    Inheritance of **212**
    Larger 208
    Seeds 206
    Simple recessive to normal A_nA_n 212, 225
    Small 208
  Breeding 238
    For economic characters 257
    Literature 238
    Materials and methods **239**
  Carbohydrate in waxy maize **568**–572
  Chlorophyll degeneracies 252
  Corn smut, 252
  Crop improvement problems 237
  Cross-pollination effect 239
  Crosses 212–236, 561, 566
  Crossing over **597**–601, 598
  Crossing over, frequency in microspore and megaspore **597**–601
  Dextrins chemical tests for 568, 569
  Dextrins rare in tissues 568
  Dominance of low protein over high 251
  Dwarf anther ear 225
    Description 207–210
    Double recessive 224
    Infertility 210, 225
    Mature plant 210
    Simple recessive to normal DD 211, 225
  Dwarf type **203**–236, 207, 208, 224, 225
    Characteristics **204**–210
    Height 218
    Inheritance **210**–212
    Seeds 206
  Ear types 205
  Endosperm 527, 570
  Endosperm of waxy maize, erythrodextrin 568–570
  Factors 218, 220, 225, 559, 560, 567
  Genetic interrelation of dwarf and anther ear types **212**–218
  Genetics 237, 571
    Protein content 238
  Growth factors 220–222, 226
  Height segregation 224
  Height 223
  Heterotic effect of cross-pollination on protein content 248, 251
  High and low races 237

Maize (*continued*)
High protein races 237, 238, 242, 253
High protein×low protein F_1 249
Inheritance of protein content **251**–252
Inheritance of zigzag culms **559**–567, **560**–565
Linkage 225, 226, **565**–567, 597–601
Low protein races 237, 248
Mass breeding, difficulties in technique 239
Mode of growth 560
Multiple factors affecting height growth 221
Normal 207, 224, 225
Heights 218
Oil content high and low races 237
Perfect flowers 203, 225
Pre-Columbian occurrence in Asia 568, 572
Production of high protein **237**–257
Protein content 239, 240, 241, 252–254, 256
Analyses 239
And cultural conditions **239**–242
And number of seeds per ear **242**–248
And yields compared 257
Comparison in self-pollinated and wind-pollinated **248**–251
Crosses between high and medium protein races 251
High and low races 237, 238, 242, 253
Of self-fertilized ears and protein in progeny 241, 242
Yields and shelling percent compared 256
Pseudo-starchy endosperm 571
Ratio modified 561, 567
Root rot 252
Rudimentary stamens **224**–225
Seedlings of various types 209
Selection experiments 237
Selection possibilities 237
Self-fertilization and isolating races for protein content 251, **252**, 253
Self-fertilized lines and use in improvement **252**–257
Self-fertilized lines decrease in yield 250
Self-fertilized lines increase of protein content 251, 254
Self-fertilized strains and resistance to plant diseases 252
Semi-dwarf andromonoecious 203
Strains
Illinois high protein 255
King Phillip Flint 240, 242, 247, 249, 253
Leaming 247, 255
Longfellow 249
Mercer Flint 243, 247, 249, 253
Minnesota No. 13 240, 241, 243, 244, 247–251, 253–257
Missouri dent corn 559, 566
Red Flint 240, 247, 250, 251
Rustler dent 240, 244, 247, 249, 253
Studies reviewed **238**
Variety, a synthetically produced 255, 256
Tall normal 208, 219
Tom Thumb pop corn 208, 218–220, 222, 559, 566
Tom Thumb ear type 205
Tom Thumb mature plants 208
Variability in stature **218**–224
Waxy endosperm
Description 568
Inheritance 569
Simple recessive to corneous 570
Waxy maize a mutation 571
White forms, three distinct recessive 424
Zigzag culms **560**, 566
Mass breeding technique 239
MASSACHUSETTS AGRICULTURAL EXPERIMENT STATION 448, 463
MAST, S. O. 144, 176, 181–*183*
Matroclinous inheritance in maize endosperm 527
MATTOON, E. W. 2, 6, 19, *115*
MAY, H. G. 3, 7, 8, *115*
Mendelian inheritance of patterns of pigeons 468
Mendelian methods and production of high-protein maize **237**–257
METZ, C. W. 336–338, 340, 342–344, *372*, 377–*379*
MEYER, ARTHUR 569, *572*
MIDDLETON, A. R. 144, 175, 176, *183*
MILL, JOHN STUART 260
MINNESOTA EXPERIMENT STATION 237–239, 251, 257
MISSOURI AGRICULTURAL EXPERIMENT STATION 559
Modifier in *Drosophila obscura* 344
MOHR, O. L. 354, *379*, 386, *425*
Monotropa Hypopytis 569
MONTGOMERY, E. G. 203, *226*
MOORE 466, *507*
MORGAN, T. H. 5, 144, *183*, 333, *334*, 355, 361, 373, 378, *380*, 386, 388, 389, 391, 396, 397, 411, 412, *425*, *426*, 527, *551*
MULLER, H. J. *334*, 373, *380*, 386, *425*, *426*, 528, 530, 545, *551*
Multiple allelomorphic series in Bruchus 484
Multiple factors 530
Mutability of *Drosophila obscura* 335, 339
Mutations
Black and black blue-tail in pigeons 486
By recombination 423
Dependent on environment for development 319, 322–330
Diversity of order of genes in different species 379
Identical in various Drosophila species 339, **341**–342, 379
In Drosophila 391
In *Drosophila hydei* **319**–334
In Drosophila species compared 375
In Helminthosporium 182
In lower animals 182
In Pestalozzia 167, 171, 182
In polyploid species 528
In yeasts 182
Method for determining identicity in different Drosophila species 376
Non-disjunctional 144
Point 423

Mutations (*continued*)
Frequency of Drosophila 112
Rate of in Drosophila species 339
Similar in different species of Drosophila 376–378
Somatic 144
Myopia 588

NÄGELI 569
NAKAO, M. 514, *551*
NEUMEISTER 473
Neuritis optica 588
NICE, L. B. 428, 442–*444*
Nicotiana hybrids 540
Sterility and incompatible chromosome combination 540
Nicotiana pollen 545
Nicotiana tobaccum, two genetically distinct red-flowering forms 424
NILES, HENRY E. **258**–273
NILSSON-EHLE, H. 530, *551*
NIXON, CLARA 274, 276, *318*
Non-disjunction 527
Absence in *Drosophila obscura* 339, **340**
Non-heritable fluctuation in *Drosophila melanogaster* 84
NONIDEZ, J. F. 403, *426*
NUTTAL, J. S. W. 476, 507
Nystagmus 588

Oena capensis 502
Oenothera brevistylis **590**–596
Factors for style length and stigma structure of slight variability 596
Fertility not due to heritable factors 590
Seeds, treatment to secure complete germination 592
Selection based on performance 591–595
Selection for style length and fertility **590**–596
Results 594
Sterility 590
Style length not due to heritable factors 590
Oenothera chromosome number 526, 528, 533, 545
Oenothera gigas 526, 528, 534, 545
Nanalla mutants of 528
×*Oelata rubricalyx* 534
Oenothera Lamarckiana 526, 534, 590
×*O. gigas* 531
Oenothera lata×*O. gigas* 531
Oenothera lata-like 534
Oenothera lata rubricalyx 534
×*rubricalyx* segregate 534
Oenothera mutants causes 530
Oenothera rubricalyx×*O. gigas* 534
Oenothera semilata 534
Oenothera sterility 533
In pentaploid species 534
Oestrous cycle lengthened by alcohol treatment 137
OHIO AGRICULTURAL EXPERIMENT STATION 508
OHIO STATE UNIVERSITY 573
OLSON, P. J. 239

Ontogenetic development of characters 2
Orthogenesis in pigeons 468, 484–486, 506
Oryza sativa glutinosa 569
OSGOOD, DR. 506
OSLER, WILLIAM 574, *582*
OVERTON, E. 514, *551*

Panicum miliaceum glutinosum 569
PAPANICOLAOU, G. N. 126, 131, 134, 136, *141*, 428, 442, *445*
Paramecium 142, 144, 149
Selection 143
PARKER, J. H. 536, *551*
PARNELL, F. R. 545, *551*, 569, *572*
PASTEUR INSTITUTE 573
Path coefficients **258**–273
Causation **258**–273 259
Coefficient of correlation 262, 269–271
Coefficient of determination 262, 270, 271
Gaussian curve of error 262
Mathematical measure of causation 258
Mathematics of **263**
Method **261**–263, 273
Test of **268**–273
Normal curve of error 262
Partial correlation 273
PEARL, R. 122, 123, 134, 137–*141*, 274, 276, 297, *318*, 428, 440, 443–*445*
PEARSON, KARL 143, 144, 156, *183*, 259, 260, *273*, 280, 301, *318*, 557, *558*
Pentaploid hybrids sterility in Oenothera, Datura and Triticum 534
PERCIVAL, J. 514, 515, 541–543, *551*
Pestalozzia Guepini **142**–201, 145, 146, 149, 157, 159, 162, 175, 181, 182
Aberrant form 171
Advantages for selection studies 149
Culture methods 150, 151
Description 145
Heritable characters 151
Intermediate line 154, 161, 184–201
Mutation 171
In length of spore appendages **167**
Mutations give rise to lines significantly different 182
Results of selection within pure lines **142**–201
Selecting device for isolating spores 168
Selection according to progeny performance **152**–167, 182
Selection biometric study 166, 188, 201
Selection effect 161, 162, 170
Selection for length of spore appendages **162**–167
Selection for length of spores **158**
Selection method 180
Selection, minus 154, 156, 160, 161, 170, 172–174, 182, 184–201
Selection of spores according to visible characters **167**–174
Selection, plus 154, 156, 160, 161, 170, 172–174, 182, 184–201
Selection totally ineffective 182
Spore appendages length 148

Xestalozzia Guepini (continued)
Spore appendages mean lengths 163–166, 189
Standard deviations 189
Spore length 147, 171, 174
Means 160, 161, 184
Standard deviations 184
Spores variability 151
Variability in number of spore appendages 152
PHILLIPS, JAMES MCILVAINE 573–582, 575, 582
PIETERS, A. J. 150, *183*
Pigeons, inheritance 466–506
Bar dominant to barless 484
Barred 467, 472, 483, 487, 495, 498, 506
Bars produce only bars 477
Black and black blue-tail dominant mutations 486
Black baldheads 500
Black blue-tail 469–471, 480, 482, 483, 485
Black check 485
Black, check and bar genetic relationships 473–480
Black, check and bar phenotypic differences 473
Black dominant to check 475
Black 467, 485
Full black 469, 470, 480, 482
Dominant to barred type 474, 475
Black-tailed birds rump color condition 496
Blacks throw blacks, checks, and bars 477
Blue 466, 467, 469
Blue barless 469, 472, 473, 485
Eichbuhlertaube 473
Feld-Tauben 473
Goldgimpel 473
Homer 473, 482, 484, 506
Ice Pigeon 473
Inheritance 484
Pfaffen 473
Strasser 473
Swallow 473, 484
Swiss Pigeon 473
Blue black-barred 466, 467, 469, 472, 473, 480, 485
Blue corresponds to "gull gray" 472
Blue with black check-marks 467
Bluing series 469–473
Check and bar independent Mendelian inheritance 468
Check and bar relationships 468, 469
Check and bar two types in domestic pigeons 501
Check and black blue-tail distinguished 482
Check breeding behavior 483
Check dominant to bar 476
Check 466, 467, 469, 471, 472, 480, 487, 495, 498–501, 506
Checked and barred reversions 468
Checked and barred due to factor recombinations 468
Checks throw only checks and bars 477
Color modification of depth and sheen in black birds 498
Color patterns in pigeons and doves correspond 502
Color types in pigeons epistatic inheritance 469
Colors due to interaction of factors 501
Columba livia progenitor of domesticated pigeon 468
Crosses 478–481, 484, 487, 492, 493, 500, 501
Dilute series 486
Dun checks 486
Dun silver-tails 486
Dun wing bars 486
Full-duns 486
Silver barless 486
Silvers 486
Sootied silvers 486
Dull-black 497–501
Dun checked 498
Epistatic series 480–486, 487, 499, 500, 502, 503
Factors 474, 480, 482, 486, 494, 497, 506
Fantails 482
Genetic relations of blue types to black 482
Helmet 466
Interaction of factors 469
Jacobin 466
Kitiness 469
Light and uniform colored rump 494–497
Orthogenesis 468, 484–486, 506
Patterns two color relationships 466
Pigeon of Barbary 466
Polyphyletic origin of domesticated pigeon 505
Red and yellow 487
Red-barred 487
Red-checked 487
Restricted reds 487
Reversionary blues 471, 480
Reversions 468
Rock-Fantail 472
Rock Pigeon 471, 486, 487, 505
Rump color conditions, genetic analysis 496
Rump color inheritance due to interaction of factors 497
Rump colors
Blue 494, 495
Black 495, 497
Dark blue 495, 497
Light blue 495
Silvery blue 495
Uniform blue 495
Recessive 496
White 494, 495, 497
Dominant to blue 496
Segregation 475
Selection experiment 468, 484–486
Self-black Tumbler 500
Sooty 469, 471, 472, 483, 485
Species 467 (See Columba)
Differences based on single factors 505
Spot 466
Tumblers 482
Typical blue or silver tail 498

Pigeons (*continued*)
Variation in color of outer vanes of outer tail feathers **487–494**
White 467, 486, 487
White spotting 469
WHITMAN'S results 469
PLATE, L. 583, *589*
PLOUGH, H. H. *334*, 338, 373, *380*
Pollen grains in parents and F_1 hybrids in wheat **523–526**
Pollen grains segregation in F_1 rice hybrid 545
Pollen of F_1 plants of species hybrids 545
Polymorphic species of domesticated plants and animals 423, 425
Polyphyletic origin domesticated pigeon 505
Polyploid species chromosome behavior 531–533
Polyploid species crosses between in wheat 530
Polyploid species genetic behavior **527–530**
Polyploid species results of crossing 529
Polyploid species of wheat sterility 533
Polyploidy correlation with multiple factors 540
Polyploidy in plant species **526**, 527
POPE, M. N. 239
Presence and absence theory 424
Primula kewensis 526
Primula sinensis 597
Primula tetraploid 528, 530
Primula flower color 333
Protein content of maize 238
Protozoa 145
Pure line hypothesis still valid 181
Pure line problem 175
Pure lines, results of selection in *Pestalozzia Guepini* (which see) **142–201**
Pygaera curtula L.×*P. anachoreta* F. F_1 532

QUINCKE, HENRICUS 574, *582*

Random mating 508–511
Ratios modified in wheat 540
Rats, white
Alcoholism and growth **427–445**
Alcohol as selective agent 134
Alcohol effect on number and size of litters 117
Alcohol treatment reduces number of young produced 139
Drunken by inhalation 123, 140
Fertility 125
Criteria of influence of alcohol treatment **124**
Greater in tests than in controls in later generations 134
Germ cells inferior eliminated by alcohol 134
Germplasm modification due to alcohol 118, 139, 140
Infertility eliminated by alcohol 118
Litter number decreased by alcohol 140
Litter size 126
Increased in treated males 136
Of treated rats reduced 129, 130, 132, 135, 140, 141
Litters number compared in guinea pig and rat treated with alcohol 137
Litters of treated rats increased number in later generations 134
Modification due to alcohol 141
Oestrous cycle lengthened by alcohol treatment 137
Rats, offspring of alcohol treated genetically superior to controls 441
Rats, resistance to effect of alcohol 136
Selective elimination due to alcohol **139–141**
Treatment of rats 122
WISTAR defectives 124, 127
RAY, JOHN *507*
Recessive factors effective in presence of dominant 545
Recessive factors in excess may be dominant over normally dominant factors 527
Recessive genes two dominate the normal 527
Recombination, origin of characters by 422
Reduction divisions in wheat and rye 548
Reduplicated chromosomes 527
RHODE ISLAND AGRICULTURAL EXPERIMENT STATION 469
RHODE ISLAND RED breed of fowl **446–465**, 447, 448, 452, 463
RICHARDS, M. H. *380*
RIDDLE, OSCAR *507*
RIDGWAY 472
ROBERTS, ELMER 333, *334*
ROBBINS, RAINARD B. **508–512**
ROOT, F. M. 143, 144, 175, 176, 181–*183*
Rosa, chromosome number 526, 531–534
Rosa hybrids 532
Rosa Sabini (*R. pimpinellifolia*×*R. sylvestris*) 532
ROSENBERG, O. 526, 531, 535, *551*, *552*
ROSSI, GILBERTO 584
RÜSSOW 569
Rust resistance in wheat 514
Rye chromosomes 519, 547

SACHS 569
SAKAMURA, T. 514, 515, 517, 543, *552*
SALVADORI, T. 467, 495, 505, 507
SAX, KARL **513–558**, 514, 536, *552*
SCHACHTZABEL E. 473, *507*
SCHLOSS, OSCAR M. 573, *582*
SCHOFIELD, RICHARD 583, *589*
Secale cereale 547
Seeds 269
Number of ovules per pod 269, 271
Number per pod 269, 271
Pods per plant 271
Seeds treatment to secure complete germination 592
Weights 269, 271
Segregation in pollen grains in F_1 rice hybrid **545**
Selecting device for isolating spores 168
Selection
According to progeny character 176
As factor in evolution 175

Selections (*continued*)
By elimination of hereditary factors in Drosophila 113
Choice of seeds from dominant plants 512
Effect of evidence wanting 181
Effect of in Drosophila 114
Nature of 113
Effectiveness in bar eye Drosophila 112
Effects conflicting evidence 143, 144
Experiments in maize 237
Experiments in pigeons 468, 484–486
Factors influencing results of 174
For eye facet number in *Drosophila melanogaster* 1–115
For length of spores **158**–162
For style length and fertility of *Oenothera brevistylis* **590**–596
Germinal changes during course of 2, 78
In an allogamous population **508**–512
In Arcella 176, 178, 179, 181
In Centropyxis 176, 181
In Didynium 176, 181
In Difflugia 178, 179, 181, 182
In Paramecium 182
In Stylonychia 144, 175, 176
Ineffective 143
Mass results 176
Method 180
Of spores according to visible characters **167**–174
Positive results by conserving mutations 4
Possibilities of 237
Result negative 174
Results 177–180
In Pestalozzia 175
With Difflugia 144
Within pure lines of *Pestalozzia Guepini* (which see) **142**–201
Selections eliminating germinal factors, effective 112
Selective effect of alcohol on rats 440, 441
Selective elimination due to alcohol 139–141
Self-fertilization producing disease resistant races in maize 252
Self-fertilized lines in maize improvement **252**–257
Sex character, secondary 583
Sex-linked characters in Drosophila 583
Sex-linked characters in *Drosophila obscura* **335**–384
Sex-linked characters in man 583
None behaves as sex-linked characters in all families 588
Three principles 588
Sex-linked groups of Drosophila species compared 373
Sex-linked heredity 583
Sex-linked mutant for *Drosophila repleta* 320
SEYSTER, E. W. 3, 8, 16, *115*
SHAMEL, A. D. 543, *552*
SHEPPARD'S tables 156
SHULL, G. H. 253, 530, *552*
Ski not a monogenic character 399
Ski wings in *Drosophila melanogaster* **385**–426
SMALLEY, F. W. 468, 475–477, *506*
SNYDER, LAURENCE H. 427
Somatic development and parental sets of chromosomes in F_2 hybrids 558
Sorghum vulgare glutinosum 569
Species crosses in wheat 553
Species differences in pigeons based on single factor 505
Species groups in wheat antiquity of 541
Species hybrids in animals chromosomes behavior in F_1 532
Species hybrids in wheat **513**–552
Behavior of F_1 chromosomes in reduction division 515, 517, 518
Chromatic bodies in microspores 515
Chromosome number 525
Chromosomes in sterile and partially sterile **520**–521
Correlation between chromosome number and fertility in F_4 515
Sterile **535**
Variation in chromosome number 515
Species polymorphic wild and domesticated 425
Species polyploid genetic behavior **527**–530
SPILLMAN, W. J. 514, *552*
STAPLES-BROWNE, R. 468, 471, 472, 475–477, 480, 486, 496, 497, 507
Sterile F_2 due to vegetative development and gametic sterility 558
Sterility and chromosome relationships 553
Sterility and quantitative relations between univalents and trivalents 536, 537
Sterility and reduplication of single chromosome 534
Sterility in wheat hybrids **513**–558
Cause 536, 537, 540, 549
STEVENS, F. L. 182, *183*
STOCKARD, C. R. 122–124, 126, 131, 134–136 139, *141*, 428, 442, *445*
STOCKING, RUTH J. 144, 175, *183*
STURTEVANT, A. H. 319–321, 333, *334*, 337, 338, 371, 373, 376, 378, *380*, 386, 391, 397, 423, *426*, 535, *552*
Stylonychia **144**, 175, 176
Response to selection 175
SURFACE, F. 274, 276, 297, *318*
Swertia perennis 569

TÄCKHOLM, G. 526, 531, *552*
TAHARA, M. 527, *552*
TEGETMEIER, W. B. 467, *507*
Temperature effect on inheritance of flower color 333
Tetany 581
Tetraploid forms 526, 527
Of tomato and nightshade 543
Originated by chromosome duplication 540
Reduction 540
Tetraploidy in wheat species origin **540**–543
Tetraploidy value **543**, 545
THATCHER, L. E. 508
THOMPSON, D. H. 1, 70, *115*
TICE, S. A. 5, *115*
TREUB 569

Triploid hybrids 533
Triploid individual 534
Triticum (see wheat)
Triticum aegilopoides 542
Triticum aegilops 516
Triticum aegilops cylindrica 541
Triticum aegilops ovata 525, 541
Triticum aestivum subsp. *durum* 516
Triticum aestivum subsp. *vulgare* var. *compactum* 516
Triticum aestivum subsp. *vulgare* var. *Spelta* 516
Triticum aestivum subsp. *vulgare* var. *turgidum* 516
Triticum dicoccoides 541, 542
Triticum sativum, *T. aestivum* subsp. *vulgare* var. *erythrospermum* (Preston) Körn *albidum* Körn (Amby) (Bluestem) 516
Sterility in pentaploid forms 534
Einkorn group 513, 516, 517, 525, 526, 534, 541, 542
Triticum monoccocum 513, 514, 516, 517, 542, 544, 546
Var. *Hornemanni* 516
Emmer group 513, 516, 518, 519, 525, 526, 534, 537, 539, 540–542, 544, 547
Triticum dicoccum 513, 514, 518, 542
Triticum durum 513–516, 518, 542, 553
Triticum polonicum 513, 514, 516, 518, 542
Triticum pyrmidale 542
Triticum turgidum 513, 514, 516, 518, 542, 546
Vulgare group 513, 516, 518, 519, 525, 526, 534, 537–542, 544, 547
Triticum compactum 513, 514, 516, 542
Hybrid origin of 541, 543
Triticum Spelta 513, 514, 516, 518, 542
Triticum sphaerococcum 542
Triticum vulgare 513, 514, 516, 519, 525, 542, 553
Sterility in pentoploid forms 534
TSCHERMAK, E. VON 514, *552*
TUPPER, W. W. 545, *552*
TURPIN, C. 275, 277, *317*
Turtur lugens 502
Turtur turtur 502

UNIVERSITY OF ILLINOIS 1
UNIVERSITY OF MICHIGAN 142, 590
UNIVERSITY OF MISSOURI 559
UNIVERSITY OF WISCONSIN 466
Urticaria 575, 581
UTAH AGRICULTURAL EXPERIMENT STATION 277

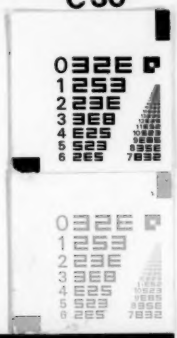
VALENTI, ANNA LOUISA 588, *589*
VANDER VEER, ALBERT JR. 576, *581*
VAVILOV, N. I. 514, *552*
VICARI, E. M. 117, 122, *141*, 427, 435, *444*
DE VRIES 528

WALDECK, MRS. 506
WALKER, ISAAC CHANDLER 574, *582*
WARNER, D. E. 275, *317*, 446, 447, 452, 464, *465*
WEATHERWAX, PAUL 203, *226*, 568–572
WEINSTEIN, ALEXANDER 419, *426*
WENE, ELMER H. 277, *317*
Wheat
Assortment of chromosomes 540
Bud mutations associated with tetraploidy 543
Cause of sterility in wheat hybrids 536, 540, 549
Cell division in species 544, 546, 548
Chromatin granules outside of nuclei in pollen grains 521
Chromosome behavior and origin of species 514
Chromosome duplication 550
Chromosome linkage 539
Chromosome number and adaptability in species 542
Chromosome number and cell size correlated 519, 523, 540
Chromosome number and size of pollen grains 523–526, 549
Chromosome number and sterility 534
Chromosome number in species 514, 525, 540, 541–543, 547, 553, 557, 558
Chromosome reduplication 540
Chromosome complete set necessary for gametic and somatic development 537
Chromosomes in sterile and partially sterile hybrids 520–521
Chromosomes of species 514, 517–521
Correlation between chromosome number and fertility in F_2 515
Correlation between sterility and vegetative development 535
Correlation between grain weight and sterility 557
Correlations in hybrid sterility in wheat 514
Cytological methods 517
Endosperm 553, 554, 556, 558
Endosperm development and sterility 553–558
Endosperm formation not due to triploid condition 558
Grain 555
Variability and chromosome numbers 558
Heterozygosis and pollen variability 525–526
Hexaploidy origin 540, 541
Hybrids 513, 514, 516, 520–525, 530, 531, 534, 535, 538, 539, 546, 547, 549, 554, 557
Intermediate chromosome numbers absent 549
Linked groups 538
Modified ratios 540
Pollen grains in parents and F_1 hybrids 523–526
Polyploid species sterility 533
Polyploidy in plant species 526–527
Reduction divisions 548
Seeds weight and sterility 553, 554
Segregates 549
Somatic development and parental chromosomes in hybrids 558
Species groups, antiquity 541

Wheat (*continued*)
Species, group differences 541
Sterility 536, 538, 549, 555
Sterility and chromosome relationships 553
Sterility and vegetative development 557
Sterility groups 525, 541
Sterility in hybrids 513–558
Sterility of species hybrids 549
Tetraploidy origin 540, 541
Variability 542
Variation in chromosome number 515
White Leghorn breed of domestic fowl, 446–448, 451, 452, 454, 463, 465
WHITMAN, C. O. 468, 472, 476, 477, 484, 486, 496, 505–*507*
WHITMAN's results interpreted on genetic basis 469
WHITMAN's selection experiments 504
WIEMAN, H. L. 587, *589*
WILCOX, A. N. 247
WILLIAMS, C. G. 508
WILLOUGHBY, F. 466, *507*
WILSON, E. B. *380*
WINKLER, H. 543, *552*
WINTON 239
WISCONSIN AGRICULTURAL EXPERIMENT STATION 469, 474
WISTAR INSTITUTE 118, 124, 127
WOLLENWEBER, H. W. 150, *183*
WRIGHT, SEWALL 258, 261–265, 267–269, 271, *273*

YAMAGUCHI, YASUKÉ 569, *572*
YULE 263

ZADE *552*
Zea mays, see maize
ZELENY, CHARLES 1–115, 2, 4, 6–8, 13, 19, 31, 84, *115*
Zenaidura macroura carolinensis 502
Zygotes eliminated by alcohol 140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